THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

Announcement: Invited Papers

At the suggestion of certain of the editorial board and other members, we have invited over 40 leading biologists who employ lepidoptera to present papers reviewing work in their field of speciality. Most of these individuals agreed to submit such papers, which will summarize their recent research. Particular emphasis will be on the general biological significance of their work as exemplified using lepidopterous material, with their methodologies described in detail. For the most part the papers will be concerned with principles and not specific systematic treatments. Motivation for the series is to acquaint the entire readership of this Journal with the diverse application of lepidoptera to investigations of fundamental biological problems and to identify workers in various disciplines who use lepidoptera as their subject matter.

The series is designed to extend over a period of several years, with two or three papers appearing in each issue. The first two papers by Nancy Stamp, and Paul Ehrlich and Dennis Murphy follow. In the near future other topics scheduled include:

Arthur Shapiro: Polyphenism and the evolution and phylogeny of the Pierids

Larry Gall: Estimates of population size and movement

Ron Rutowski: Mating behavior

Joel Kingsolver: Thermoregulation

Jane Hayes: *Colias alexandra*: a model for the study of natural populations of butterflies

Peter Brussard: Electrophoretic studies of *Cercyonis* and *Euphydryas*

Invited Paper

Interactions of Parasitoids and Checkerspot Caterpillars *Euphydryas* spp. (Nymphalidae)

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Abstract. *Euphydryas phaeton* caterpillars have a variety of escape and defensive behaviors. These behaviors vary among instars. The caterpillars can effectively ward off *Apanteles euphydryidis* wasps. These parasitoids exhibit varying attack behaviors relative to the different prediapause instars of *E. phaeton*. Comparison of *A. euphydryidis* and *Benjaminia euphydryadis* suggests that these wasps employ alternative strategies for larval parasitism of the same host. The host-parasitoid interactions described here reflect the spatial and temporal availability of the caterpillars to their insect enemies. The availability of early instar larvae spatially (at webs) varies dramatically, with periods of few larvae alternating with periods of abundant hosts.

Climatic factors affect the temporal availability of *Euphydryas* species to their parasitoids, especially *Apanteles* species with multiple generations per that of the host. Hence, parasitism was not a major factor in most population fluctuations of *Euphydryas* species, either among localities or years at sites. Other aggregated host-parasitoid systems are expected to parallel the patterns shown here, with parasitoids responding to host patches in terms of numbers of available hosts and exhibiting various search and attack behaviors depending on the changing behavior of the hosts.

Introduction

Ecological and behavioral studies of lepidopteran hosts and parasitoids interacting in natural populations are rare (Matthews, 1974; Morrison & Strong, 1980). Yet to understand how and when parasitoids are able to subdue host populations to observed or desired levels, it is necessary to determine the availability of hosts spatially and temporally relative to their parasitoids under natural conditions. In host-parasitoid systems where the caterpillars are gregarious, parasitoids may be drawn in numbers to these host patches. Consequently, interactions between the caterpillars and parasitoids may be more readily observed and correlated with population responses of the hosts and parasitoids than in systems where the hosts are solitary.

The first objective of this review is to examine Baltimore checkerspot caterpillars (*Euphydryas phaeton* Drury: Nymphalidae) and their parasitoids, as an example of interactions of aggregated lepidopteran hosts and specialist parasitoids. This system is particularly suitable for examining

host-parasitoid interactions in natural populations because: 1) the egg clusters of *E. phaeton* are easily located, 2) caterpillars construct communal webs at the tops of host plant stalks, which are about 1 m in height, making them easy to monitor and manipulate, 3) parasitoids are common and large enough that they can be observed easily at the webs and 4) activity of hosts and parasitoids is mainly diurnal. Data from recent studies are incorporated with those of published research to show that these caterpillars defend themselves against their parasitoids and the parasitoids respond accordingly. The second objective here is to compare the *E. phaeton*-parasitoid pattern with other *Euphydryas* host-parasitoid systems. This comparison indicates the constraints on these host-parasitoid interactions as a consequence of climatic factors.

The Host-Parasitoid System

E. phaeton and its parasitoids were studied at the Conservation Center at Front Royal, Virginia, from 1977 through 1981. The Baltimore checkerspots deposited eggs in clusters of about 274 (Stamp, 1982a) in June on their larval host plant turtlehead (*Chelone glabra* L.: Scrophulariaceae), which is a perennial that forms clones in wet meadows and along streams. These butterflies tend to lay their eggs with those of other females (Stamp, 1982b). As a consequence of this, coupled with egg loss from predation and parasitism of less than 10%, larval group size varied initially from about 250 to 2500 (Stamp, 1981a, b). The first three instars formed compact communal webs in July, feeding on leaves enclosed within and adjacent to their webs. Larval activity at webs varied through the day and month, with larvae molting synchronously within webs and third instar larvae spending more time outside webs as a consequence of consuming food more rapidly than first instar larvae (Stamp, 1982a). The caterpillars began diapause as fourth instar larvae in webs in early August. In the fall these caterpillars left the webs to overwinter in small groups in the plant litter on the ground (Bowers, 1978; Stamp, 1982a). The late instar larvae fed from April through mid-May and then pupated.

Apanteles euphydryidis Muesebeck (Braconidae) is a specialist larval parasitoid of *E. phaeton*, with only one other recorded host, the closely-related Harris' checkerspot (*Chlosyne harrissii*, Marsh, 1979). These wasps attacked the web-making early instar larvae of *E. phaeton* in July through early August.

Female *Apanteles* were found at 20-50% of the early instar webs (Stamp, 1982c). The wasps' attendance of the webs varied through the day, with the highest numbers of *Apanteles* searching the surface of the webs in late morning and early afternoon. Webs were attended as early as 0600 and as late as 2100, which suggests that the parasitoids remained at the webs overnight.

The parasitoids attended the webs for hours at a time, with a third of

each hour spent searching for hosts (Stamp, 1982c). When *Apanteles* on the outside of the webs located caterpillars inside the webs, they palpitated the web surface with their antennae, often turning in circles, and probed that area with their ovipositors. Usually, the parasitoids attacked the caterpillars by thrusting their ovipositors through the webbing and, if close enough, into caterpillars for a few seconds. *Apanteles* wasps also attacked larvae when they were outside the webs but considerably less often. Here a wasp carefully approached a larva from behind and thrust the ovipositor forward between her legs into the caterpillar. Generally the wasps avoided caterpillars on the outer surface of the webs, probably as a consequence of the defensive behaviors of caterpillars.

Although 42% of the emerging *Apanteles* were males (Table 1), males seldom occurred at webs (e.g. 2.8% of 142 *Apanteles* observations in 1981). Males emerged a day or two before females and most likely mating occurred at the cocoons. The occasional males at early instar webs created havoc by fanning their wings and walking over larvae to approach females; the caterpillars thrashed vigorously and the females had to retreat until the caterpillars calmed.

The *Apanteles* wasps overwintered as immatures in the diapausing caterpillars. Prediapause caterpillars dissected were parasitized 6% of the time in both 1978 and 1979 (Stamp, 1982c). In the spring the immature parasitoids ate through the cuticle of the hosts, spun cocoons and emerged as adults a week or two later. Solitary *Apanteles* exited from a few larvae in April, but most of the larvae with *Apanteles* cocoons occurred in early May, with 7.5 ($\pm$1.5 SE) parasites per host. Comparison of the means of 2.9 ($\pm$0.4 SE) parasites per diapausing fourth instar larva in August and cocoons per host both in April and May suggests that the solitary parasites emerged earlier in the spring than those aggregated in hosts. The *Apanteles* emerging in the spring attacked the late instars of *E. phaeton*. Their offspring prolonged the last host stage up to eight weeks and emerged in the summer when web-making early instars were available again. Parasitism of sixth instars prior to the adult flight period was 20% in 1979 but may vary considerably among years.

Benjaminia euphydryadis (Viereck): Ichneumonidae is a specialist larval parasitoid on *E. phaeton*, with only one other recorded host, *Chlosyne harrissii* (Carlson, 1979). These parasitoids attacked the early instars by traveling from web to web, spending less than a minute at each (41 sec $\pm$12 SE, n=5 wasps). They probed the webs, usually inserting the entire abdomen (6 mm in length with the ovipositor) into the webs at several locations. This behavior shook the webs, with many larvae responding by simultaneously and vigorously thrashing for several minutes after the wasps departed (Edwards, 1884; Stamp, 1982c). Parasitism of diapausing fourth instar larvae was 6% and 4% in 1978 and 1979, respectively (Stamp,

Table 1. Summary of patterns of *Apanteles* parasitoids using *Euphydryas* caterpillars.

Host *Euphydryas*	Parasitoid *Apanteles*	Number of Parasitoid Generations	x̄ Parasites/ Larva ± SE (n=hosts)	Host Instar Exited From	Time to Wasp Emergence from Cocoons in Weeks	% Females, with χ^2_c test for Sex Ratio (n=wasps)	Location	Reference
editha	*koebelei*	1-2	20.4 ±1.7 (40)	late	• 2	67.5 p<0.001 (815)	Jasper Ridge, Calif.	White, 1973
phaeton	*euphydryidis*	1-2	1 (80+)	4th	1	—	central Mass.	Bowers, 1979; pers. comm.
		1-2	9.8 ±2.3 (16)	6th	1	67.4 p<0.001 (141)	Manlius, N.Y.	Stamp, unpubl. data
		2 minor	1	4th	1-2	—	Front Royal, Va.	Stamp, 1982c; unpubl. data
		major	7.5 ±1.5 (37)	5th	1-2	—		
		major	28.4 ±2.7 (37)	6th	2	57.9 p<0.001 (561)		
aurinia	*bignellii*	3 major	2.8 ±0.3 (51)	late 3rd	1	—	Oxford, England	Porter, 1983
		major	3.7 ±0.2 (156)	late 4th	1-2	—		
		major	44.7 ±3.6 (41)	6th	4-7	—		

1980). *Benjaminia*, a solitary parasite, overwintered in its diapausing host. In June the mature parasite caused the cuticle of its host to puff and harden and, thus, serve as a cocoon prior to its emergence two to three weeks later.

Defense by Caterpillars and Response by Parasitoids

Often the caterpillars defended themselves from attack by parasitoids, usually by thrashing the front half of the body back and forth and occasionally knocking away wasps (Stamp, 1982c). When numerous *E. phaeton* larvae occurred in one location on webs, disturbance by parasitoids resulted in simultaneous thrashing by caterpillars. This defensive behavior lasted up to 15 min with wasps moving to unoccupied portions of the web or adjacent leaves, and many larvae moving from that area of the web. The caterpillars also defended themselves by reaching around and attempting to contact the parasitoids and regurgitate on them. The *Apanteles* wasps spent considerable time grooming after contact with defensive caterpillars.

The effect of tactile disturbance of larvae was examined in the laboratory. Stalks of turtlehead with communal webs were collected and kept in water, with fresh stalks added daily. For both second and third instars, 60 larvae were observed for one minute each to determine the behavior of undisturbed caterpillars. Then each of these 60 larvae was touched with a two-haired brush (simulating the touch of an *Apanteles* wasp palpitating with its antennae). In response to this tactile stimulation, the larval instars displayed an array of escape and defensive behaviors (Fig. 1). Third instar larvae were more likely to thrash than second instar larvae. This may reflect the body size ratio of caterpillars to their major natural enemies. For example, *Apanteles* wasps were larger than the first instar larvae, but second instar larvae were two times the size of *Apanteles* and the third instar larvae four times that of *Apanteles*. Thrashing by third instar larvae was more effective against the wasps than that by the smaller instars because third instars were more likely to knock the wasps away. In contrast, larvae of similar size to the wasps may be more effective in using regurgitation as a deterrent against these wasps than by trying to knock them away. These larvae were more likely to make immediate contact and smear regurgitate on their attackers than were caterpillars much larger than the wasps.

I also disturbed larvae in the field, but this time instead of directly stimulating larvae, each web was jabbed 10 times with a dissecting needle to create a general web disturbance, simulating that caused by *Benjaminia* wasps. For both first and third instar webs, larvae moved into the webs within three minutes after the disturbance (Fig. 2). The first instar larvae increased their thrashing significantly, whereas the third instar larvae decreased their head-jerking. Again, this difference may reflect the body size ratio of caterpillars to their insect enemies. First instar larvae may
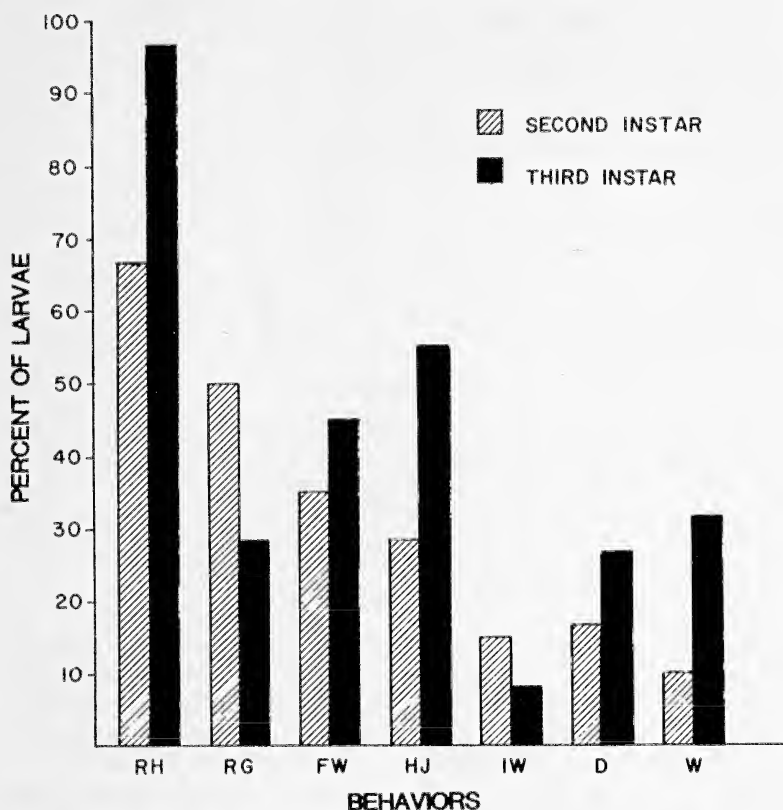
Fig. 1. Escape and defensive behaviors of *E. phaeton* larvae exhibited in the laboratory. Caterpillars were disturbed by a two-haired brush, simulating the touch of an *Apanteles* wasp. RH - reared head, RG - regurgitated, FW - walked away quickly, HJ - head-jerking, IW - into web, D - dropped from web and W - wriggled (all legs detached). Third instar larvae thrashed more than second instar larvae (χ_c^2 text, $p<0.05$). Before disturbance (not shown), none of the third instar larvae exhibited escape or defensive behaviors and second instar larvae spent less than 1% of their time in such behaviors.

benefit by reacting together to any disturbance, except when touched directly. In this case, when larvae can be easily overwhelmed by their insect enemies, catalepsis may be a more prudent behavior than thrashing (e.g. Rotheray, 1981). For instance, larval movement may trigger oviposition behavior by parasitoids (Vinson, 1976). Also, predatory pentatomids were more likely to encounter active tent caterpillars (*Malacosoma californicum*) than inactive ones (Iwao & Wellington, 1970a). *E. phaeton*

Fig. 2. Response by *E. phaeton* larvae under field conditions to general web disturbance, simulating that caused by *Benjaminia* wasps. Solid lines indicate first instar larvae, whereas dashed lines show third instar larvae. Bars indicate ± one standard error. Number of larvae outside of webs before and after disturbance are shown (Wilcoxon paired-sample tests with n=20, p<0.001) as are number of larvae head-jerking before and after disturbance (p<0.001).

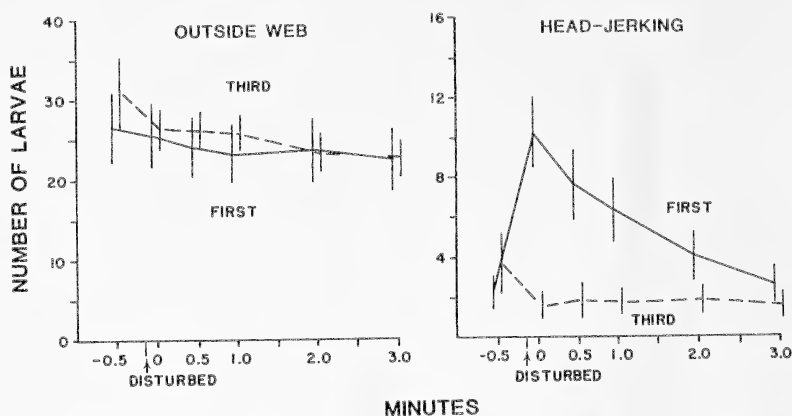third instar larvae were more likely to defend themselves effectively against insect enemies than were first instar larvae. Consequently, third instar larvae may spend more time feeding and less energy on defense by reacting to offensive tactile stimuli rather than to a general array of stimuli, such as shadow and web disturbance, as the first instar larvae do.

In addition to differences in defensive behaviors among instars, the instars varied in terms of potential defensive structures on their bodies. First instar larvae had sparse setae, whereas second through sixth instar larvae had rows of tubercles with spines radiating at 45° angles. By the third instar, the combination of tubercle and spines was similar in length to that of the ovipositor of the *Apanteles* parasitoids and, thus, may have deterred penetration of the ovipositor as well as serve as sensory devices (Table 2). Ayre and Hitchon (1968) found differences in the setae covering tent caterpillar instars (*Malacosoma americanum*), with ants unable to attack densely-haired late instars successfully. Thus, such body structures may be effective defensively when the body size ratio of caterpillar to insect enemy is relatively large (e.g. greater than two).

To examine the interactions of checkerspot caterpillars and the parasitoid *Apanteles euphydryidis*, 20 wasps were observed at first instar webs in the field and six each, at second and third instar webs. Comparison of the prediapause instars indicated that *Apanteles* wasps encountered these larvae outside the webs at a similar rate (Fig. 3). However, the wasps seldom attacked first and second instar larvae outside the webs (less than

Table 2.   Comparison of the lengths of potential sensory and defensive
structures on *E. phaeton* larvae to ovipositor lengths of *Apanteles
euphydryidis*. The tubercle-spine length of the third instar
larvae was similar to the ovipositor length of the wasps and the
tubercle-spine length of fourth instar larvae was greater than
the ovipositor length (Stamp, 1982c).

| | Setae of first instar | Tubercle-spine of | | | Wasp ovipositor |
		second	third instars	fourth	
x̄ length in mm	0.16	0.29	0.78	1.00	0.76
SE	0.01	0.02	0.01	0.02	0.01
n	30	30	30	33	30
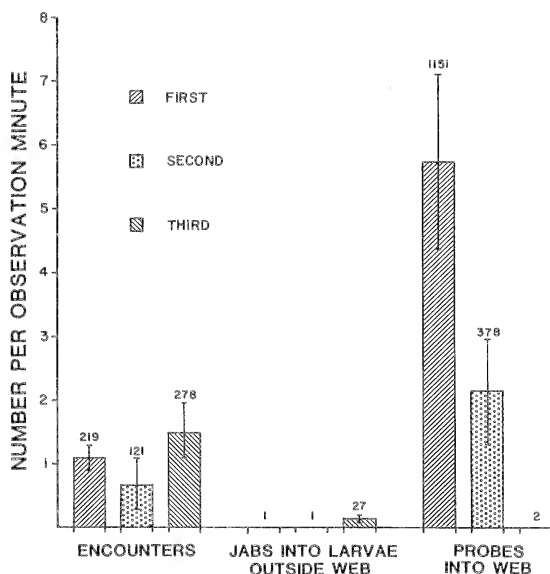
Fig. 3.   Interactions of *E. phaeton* larvae and *Apanteles euphydryidis* in natural
populations. Responses by parasitoids at webs of first, second and
third instar larvae are show. Bars indicate ± one standard error and
numbers show total parasitoid observations per category. "Encounters"
are between parasitoids and caterpillars on the outside of webs and
were similar among instars (Kruskal-Wallis text, v=2, p>0.05). Jabs
into larvae outside webs and probes into webs varied among instars
(Kruskal-Wallis tests, p<0.01).

1% of the encounters) but often jabbed at third instar larvae there (10% of encounters). In contrast, the wasps probed most at first instar webs and least at webs of third instars. These differences in response by the wasps to the caterpillars suggest again that defensive behaviors varied among the host instars.

Some *E. phaeton* larvae tried to escape when disturbed, by crawling away quickly, often into the web, or by dropping from the web, usually on a silk thread (Fig. 1). To determine how webs might protect larvae from parasitism, I damaged webs by making small holes in them and then monitored activities of caterpillars and parasitoids (Stamp, 1981a). Larvae in the outer portion of the damaged webs exited from the webs and joined those larvae on the outside of the webs. Damaged webs were repaired, usually within 24 hours. But parasitoid access to larvae by damaging the webs did not increase the level of parasitism. In fact, fewer parasitoids were found at the damaged webs compared to undamaged webs. It appears that the parasitoids did better when they could attack larvae through the webbing, and perhaps avoid the defensive responses of larvae. Most likely webs were important, at least relative to these parasitoids, when the larvae were molting. At that time the caterpillars were deep within the webs, usually surrounded by frass and layers of webbing. In large webs, molting caterpillars were out of reach of both the major larval parasitoids.

Example of an Aggregated Host-Parasitoid System

These studies show that *E. phaeton* caterpillars exhibit a variety of escape and defensive behaviors, these behaviors vary among instars and *Apanteles* parasitoids respond accordingly. In addition to behavioral differences among instars, molting caterpillars are less defensive than active caterpillars and molt synchronously in the core of the web. This suggests that the number of available, non-parasitized caterpillars per web may fluctuate sharply, with periods of relatively few available individuals at a web alternating with periods of abundant hosts (Stamp, 1982d). Attendance of webs by parasitoids should reflect this fluctuation in host availability, with webs of molting caterpillars unattended by *Apanteles*. Some indirect evidence, that *Apanteles* wasps were moving among webs more frequently than expected (Stamp, 1982d), supports this contention. In contrast, *Benjaminia* wasps which are larger and reach farther into webs than *Apanteles* may be less constrained by such changes in host availability.

Many aggregated host species exhibit defensive behaviors and fluctuating numbers of available hosts, due to molting in protected locations and perhaps latter instars defending themselves more effectively than early instars. For example, Iwao and Wellington (1970b) found that tent caterpillars differed in their behavior, with inactive types less defensive and parasitized more frequently. Active fifth instar larvae were generally

aggressive enough to ward off predatory pentatomids, whereas other, smaller instars were not (Iwao & Wellington, 1970a). Other lepidopteran species have been reported defending themselves effectively against insect enemies (Smith *et al.,* 1955; Morris, 1963). Therefore, such host-parasitoid systems may be similar to that of *E. phaeton,* with parasitoids responding to host patches in terms of the numbers of available hosts rather than absolute numbers of hosts and exhibiting different attack behaviors relative to host instar and activity.

E. phaeton larvae are similar to some other aggregated lepidopteran species in that they overwinter as mid-instars. Consequently, vulnerable larvae are available during two distinct periods, even though this species is univoltine (Fig. 4). Caterpillars are present for about five weeks in the summer and four to six weeks in the spring, with a gap of four to six weeks between late and early instars in early summer (during pupation and adult flight period; Bowers, 1979; Stamp, 1982c).

One parasitoid attacks hosts at these two larval periods whereas the other does not. The *Apanteles* wasps have a generation at each larval host period, which is regulated by their laying numbers of eggs to suit the size of larval stages involved. In contrast, the *Benjaminia* parasitoids have one generation per that of the host. *Benjaminia* are four times the length of *Apanteles.* Consequently,*Benjaminia* immature parasites require more food than a single *Apanteles* and thus they must complete their development in a later instar. This contrast in solitary versus gregarious

Months

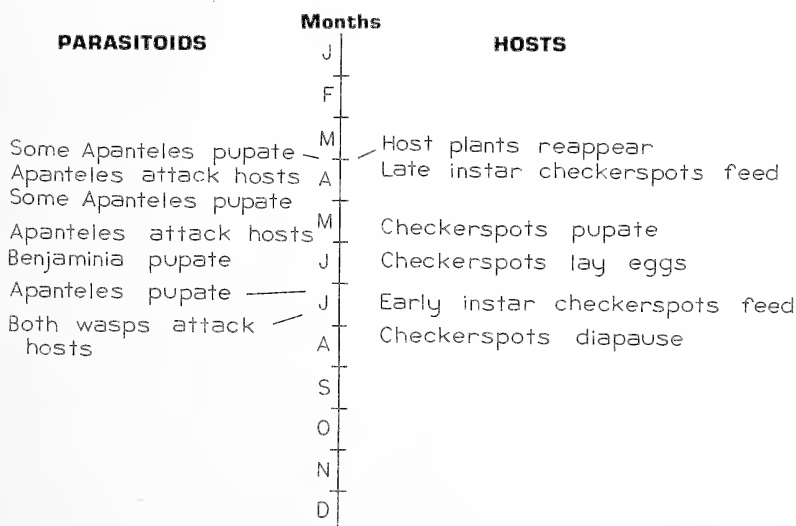| PARASITOIDS		HOSTS
	J	
	F	
Some Apanteles pupate	M	Host plants reappear
Apanteles attack hosts	A	Late instar checkerspots feed
Some Apanteles pupate		
Apanteles attack hosts	M	Checkerspots pupate
Benjaminia pupate	J	Checkerspots lay eggs
Apanteles pupate	J	Early instar checkerspots feed
Both wasps attack hosts	A	Checkerspots diapause
	S	
	O	
	N	
	D	

Fig. 4. Association of checkerspots (*Euphydryas phaeton*) and larval parasitoids (*Apanteles euphydryidis* and *Benjaminia euphydryadis*) in Virginia.

development by the parasites, by contributing more parasites per host and an additional generation per that of the host, should yield a larger population of *Apanteles* than *Benjaminia* in the summer. Based on the mean numbers of *Apanteles* cocoons per host per parasitoid generation in Table 1, with 57.9% of them females and 50% of those killed by hyperparasitoids (parasitoids of parasitioids; Stamp, 1981c), the number of female *Apanteles* should have been 94 times that of *Benjaminia*. Observations at webs were 100 female *Apanteles* wasps to one *Benjaminia* in July 1979 (Stamp, 1982c). That the levels of parasitism for the early instars were the same for these two parasitoids in that year when the adult numbers differed so suggests that individual *Benjaminia* may be more efficient at exploiting the host population than are individual *Apanteles*. Thus, the *Benjaminia* pattern (a solitary, large parasite per host, with one generation per that of the host) and the *Apanteles* pattern (adjustment of parasitoid numbers relative to host size with multiple generations per that of the host) illustrate a tradeoff in parasitoid packaging. This is analogous to the alternative strategies in plants, of producing either a few, large, competitive seeds or numerous, small, colonizing propagules (Harper *et al.*, 1970).

Comparison of *Euphydryas* Host-Parasitoid Systems

Euphydryas species are attacked by one to three larval parasitoids, often by an *Apanteles*, a *Benjaminia* and a tachinid species (Table 3). Generally, egg parasitism has not been reported for *Euphydryas* species, even though eggs remain on host plants for several weeks (e.g. two weeks for *E. editha*, Singer, 1972; three for *E. phaeton*, Stamp, 1981b; three to six for *E. gillettii*, Williams *et al.*, 1983; five for *E. aurinia*, K. Porter, 1981). However, *E. phaeton* egg clusters were parasitized frequently but at a low level by trichogrammatid wasps (Table 3).

Only the *Apanteles* parasitoids exhibited more than one generation per that of the host and this may vary with location (Table 1; and White, 1973). The *Apanteles* species emerged one to two weeks after spinning cocoons, except in *Apanteles bignellii* on sixth instar *E. aurinia*. Here the fully formed wasps remained in their cocoons from four to seven weeks, emerging when newly-hatched hosts were available again (Porter, 1983). In contrast, apparently the other *Apanteles* species prolonged the last host instar and then spun cocoons just prior to the availability of early instar hosts (e.g. Stamp, 1981c). The sex ratio of the emerging wasps was skewed towards females (Table 1). As newly-emerged females were likely to be mated at cocoons, fewer males may have been necessary to insure fertile (female) eggs (White, 1973). Thus, a female could increase her fitness by laying more female eggs than male ones.

The variation in parasitism among years for *Euphydryas* species was considerable (Table 3). Parasitism was cited as the major factor in marked

Table 3.   Sets of parasitoids attacking *Euphydryas* species, with some indication of parasitism levels.

Host Euphydryas	Parasitoid Species	Level of Parasitism	Location	Reference
aurinia	Apanteles bignellii (Braconidae)	1-4% late 3rd in-star 14% late 4th instar 8-75% 6th instar	Oxford, England	Porter, 1983
	Apanteles melitaearum (Tachinidae)	—	northern England	K. Porter, pers. comm.
	Erycia cinerea (Tachinidae)	—	England	
chalcedona	Apanteles koebelei	—	western U.S.A.	Marsh, 1979
	Benjaminia fuscipennis (Ichneumonidae)	—	western U.S.A.	Carlson, 1979
	Siphosturmia melitaeae (Tachinidae)	—	Jasper Ridge, CA	Brown and Ehrlich, 1980
editha	Apanteles koebelei	2-61% late instars	Jasper Ridge, CA	Ehrlich, 1965
		0-67% late instars	numerous sites in	White, 1973
	Benjaminia fuscipennis	0-25%	Calif. and Oregon	
	Siphosturmia melitaeae	0-27%		
gillettii	Benjaminia fuscipennis*	30%	Park Co., WY	E. H Williams, pers. comm.
	Peromalus vanessae (Pteromalidae)		Gunnison Co., CO	Williams et al, 1983
phaeton	trichogrammatid wasp	5%	Front Royal, VA	Stamp, 1981b
	Apanteles euphydryidis	6% early instars 20% late instars		Stamp, 1982c
	Benjaminia euphydryadis	4-6%		Stamp, 1980
	Peromalus puparum	—		Stamp, unpubl. data
	Compsilura concinnata (Tachinidae)	—	northeastern U.S.A	Arnaud, 1978

*identified tentatively by the author, based on Cushman (1933).

population fluctuations of *E. aurinia* (Ford and Ford, 1930; Porter, 1983), but it was not an important factor in population fluctuations of *E. editha* and *E. chalcedona* (Ehrlich *et al.*, 1975; Lincoln *et al.*, 1982).

This difference may reflect constraints on host-parasitoid interactions by climatic factors. In *Euphydryas* species of the western United States, these fluctuations have been attributed to the distribution, abundance and health of the host plants, which are affected severely by drought (Ehrlich *et al.*, 1980; Mooney *et al.*, 1980). For example, up to 99% of *E. editha* using *Plantago erecta* died from starvation before reaching diapause as a consequence of host plant senescence (Singer, 1972; White, 1974). Thus, larvae from eggs laid late in the spring were less likely to obtain enough food before diapause than those from eggs deposited earlier. This suggests that the parasitoids may benefit by attacking early instars when they first become available rather than throughout the spring season (White, 1973). However, with the presence of early instars as short as three weeks in duration (Singer, 1972), such synchrony by the parasitoids with their hosts (essentially with the first half of that period) may be difficult. Some evidence indicates that diapausing larvae previously parasitized by *Apanteles* are less likely to survive than nonparasitized ones (White, 1973). If few parasitized larvae survive over the diapause period, the *Apanteles* population the following spring relative to that of the host should be small.

The interactions of parasitoids and *E. gillettii* in the Beartooth Mountains of Wyoming may provide another example of limitations imposed by climatic factors. *E. gillettii* eggs hatch between early August and mid-September, but larvae hatching in September die due to the onset of winter (i.e. frosts, snow and leaf abscission of host plants, Williams, 1981). Again, the parasitoids (in this case *Benjaminia*) may benefit by synchrony of adult emergence with caterpillars hatching in August, as opposed to September. This population of *E. gillettii* larvae undergo two winters before reaching maturity (Williams *et al.*, 1983) and consequently *Benjaminia* also require two years for development (E. H. Williams, pers. comm.). The first and second instars of *E. gillettii* are available for three to four weeks (in early September), third and fourth instars for about seven weeks (late May to mid-July of the second summer) and fifth and sixth instars for four to five weeks (late May to early July in the followng year; E. H. Williams, pers. comm.). This would seem to provide ample opportunity for attack by *Apanteles*, but such parasitoids have not been found using *E. gillettii*. Perhaps the combination of a short, variable period (three to four weeks) to attack the young instars and difficulty in surviving the diapause period imposes too severe a constraint for *Apanteles* populations to use this host successfully.

Drastic fluctuations in *E. phaeton* have been noted (Bowers, 1979; Clench, 1979). Fluctuations in Baltimore checkerspot numbers have been linked to periodic flooding and presumably drowning or washing away of

caterpillars (Brussard and Vawter, 1975). In addition, defoliation of the host plants by sawfly larvae (*Macrophya nigra* and *Tenthredo grandis*: Tenthredinidae) when *E. phaeton* prediapause larvae were also feeding may contribute to high mortality of checkerspots (Stamp, unpubl. data). But flooding and defoliation probably affect parasitized and nonparasitized larvae (and consequently numbers of adult hosts and parasitoids) similarly. Furthermore, parasitism is unlikely to contribute to population fluctuations of *E. phaeton* when attack by generalist hyperparasitoids on both generations of *Apanteles* is high, as it was in Virginia (43-57% killed, Stamp, 1981c).

In contrast, climatic factors in the spring may influence host-parasitoid interactions of *E. phaeton* in the same way that they affect *E. aurinia*, a European checkerspot that uses habitats similar to those of *E. phaeton*. When air temperatures on average were low and skies clear, *E. aurinia* postdiapause larvae fed at an optimal rate, by using basking behavior to become independent of ambient temperatures (Porter, 1982). Under these conditions, *Apanteles* emerged as adults after a prolonged pupal period and when most of their hosts had already pupated (Porter, 1983). For instance, when parasitoid emergence occurred in synchrony with host availability, 75% of the postdiapause larvae were parasitized, whereas when emergence was asynchronous, the level of parasitism was only 8%. The period when larvae are present for *Apanteles* adults in the spring may be as short as a few days in some years (Porter, 1983). *E. phaeton* postdiapause larvae are subject to variable spring conditions also and exhibit basking behavior (Stamp, pers. observ.).

The major difference between these two host-parasitoid systems is that the prediapause larvae of *E. aurinia* are present for the parasitoids up to eight weeks in contrast to five weeks for those of *E. phaeton* (Porter, 1981; Stamp, 1982c). As a consequence, some *Apanteles* on *E. aurinia* reach maturity and produce cocoons in late summer, on late second and late third instars (Porter, 1983). These wasps then attack the larvae of that summer, which contributes a partial generation of *Apanteles* that does not occur in the *E. phaeton* system. Therefore, with relatively more parasitoids emerging from and then attacking hosts in the spring, especially if the climatic conditions favor host-parasitoid synchrony, parasitism of *E. aurinia* late instars may reach extremely high levels. Parasitism may cause dramatic declines in the host population, particularly if high levels of parasitism occur over consecutive years. Here the fluctuations in parasitism should correspond with the climatic patterns of spring and summer, which determine the length of the larval periods at those times.

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Invited Paper

On Butterfly Taxonomy

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In one sense taxonomy may be the most central of all sciences. In order to communicate, or even to think about anything, people are forced to categorize objects and ideas. They naturally taxonomize the world. Taxonomies may differ a great deal from person to person and from culture to culture, but the categorizing process appears to be universal.

The goals of the formal science of taxonomy are to categorize organisms into hierarchical groups on the basis of explicit criteria and to apply to those groups a nomenclature that provides accurate, unambiguous, and, as far as possible, stable designations for the groups recognized. At the moment, in botanical and zoological nomenclature these designations are various sorts of latinized names; there is, however, no theoretical reason why they could not be numbers or pictographs.

There is a great deal of debate over exactly what criteria should be used in evaluating taxonomic relationships. The fundamental information used in producing classifications is the similarities of entire organisms or of their component structures. The detailed definition and interpretation of similarities, however, can become quite complex. Many taxonomists believe that similarities themselves should not be used directly to create the classifications. Instead, they use similarities and differences to infer the branching sequences of the evolutionary lines of the organisms involved. The resulting history is then used as the basis for the taxonomy (see, e.g., Vane-Wright, 1979; de Jong, 1982). Those who pursue this methodology are called cladists.

Other evolutionists (e.g., Ehrlich, 1964; Sokal and Sneath, 1963) think that basing classification on inferred or imagined phylogenetic branching sequences weakens the usefulness of the taxonomic system. Instead they base classification solely on phenetic divergence (the amount of phenotypic difference between taxa produced by both the time and *rate* of evolution. Those who use statistical procedures to evaluate phenetic differences are known as numerical taxonomists.

The cladistic view has led to exhausting, often esoteric disputes, as a perusal of the last decade or so of the journal *Systematic Zoology* will reveal. But these arguments need not concern us here—for, in fact, most

groups of organisms are, and will continue to be, taxonomized primarily on the basis of their similarities. *Pieris* and *Colias* are both in the family Pieridae, and *Euphydryas* and *Cercyonis* are both in the family Nymphalidae because each is more similar to the other than either is to members of other families.

Systematically, the butterflies are among the best known groups of organisms. This traces back to their long-term popularity with collectors. And, because the life histories of many species have been described, at least superficially, and because butterflies are easily studied in both field and laboratory, butterflies have become a major tool for investigations of ecology and evolution.

Here we briefly look at the taxonomy of butterflies, dividing the discussion into four levels: the taxonomy of families, genera, species, and subspecies. We then consider the relationship of taxonomy and nomenclature in light of recent trends.

Families

Those working on the higher taxonomy of insects are in general agreement that the overall similarities among butterflies and certain families of moths preclude the treatment of butterflies as the once-recognized suborder Rhopalocera and the moths as a second suborder, Heterocera. The butterflies, along with virtually all moths, have been placed in the suborder Glossata, separated from the remaining most primitive moths by dramatic anatomical differences (see Kristensen and Nielsen, 1983). Butterflies and the other Macrolepidoptera, which are included in the omnibus infraorder Heteroneura, have separate openings for insemination and egg laying, well-developed proboscides, inconspicuous palpi, reduced membranous ovipositors, and heterogeneous fore and hindwing venation. Most taxonomists consider butterflies to consist of two superfamilies, the Papilionoidea, the true butterflies, and the Hesperioidea, the skippers (although Brock, 1971, includes both in Papilionoidea).

Taxonomic treatments of butterflies at the family and subfamily levels should consider diverse butterfly groups and even moth groups from a worldwide sampling of taxa. It is no coincidence that the studies of higher butterfly taxonomy utilizing the widest representation of genera (Ehrlich, 1958b; Kristensen, 1976; Scott, 1984) are conservative in their use of higher categories. All recognize four major groups of the Papilionoidea: the families Papilionidae, Pieridae, Nymphalidae, and Lycaenidae. That these four groups should be families is obvious and generally agreed upon—the members of each family share a great many features of their adult skeletal anatomy and musculature, so many that the families segregate on the basis of almost any subset of characteristics (e.g., Ehrlich, 1958a, b; Ehrlich and Ehrlich, 1967; Kristensen, 1976; Scott,

1984). Strong similarities also seem to prevail within families in the immature stages; unfortunately, these stages are much less thoroughly investigated, even though they should be no less important in formulating taxonomies than adult characteristics.

More controversial than the recognition of four families is the retention of the small group of snout butterflies as an additional family, the Libytheidae. Here we run into a problem common to all taxonomic levels. While the taxonomic and nomenclatural systems are strictly hierarchical, nature is not. Among any N taxonomic entities, there are $(N-1)/2$ sets of similarity relationships and for any phylogenetic tree, however constructed, an infinite number of levels at which branching can occur. A task of the taxonomist is to fit the most sensible possible hierarchical system of nomenclature to the perceived reality of nature. In the case of the libytheids, they are clearly more closely related to the nymphalids than to any other group. The basic question is whether they are still different enough to be considered a family. The most comprehensive studies of the higher classification of butterflies have been those of Ehrlich (1958a, 1958b) and Ehrlich and Ehrlich (1967). They made an arbitrary decision to retain the Libytheidae as a family.

Another question of familial status within the true butterflies is whether or not the four subfamilies of the Lycaenidae (Lycaeninae, Styginae, Curetinae [see Scott, 1984], and Riodininae) are sufficiently distinct to justify raising them to family level. Such justification would require very convincing new evidence showing that the differences between these subfamilies are of the same order of magnitude as those between, say, the Papilionidae and the Pieridae. Unless truly substantial information exists in such neglected characters as larval muscular patterns, it seems highly unlikely that any adequate evidence will be found. Therefore it is imperative to follow the rule that obligatory categories (in which every animal must be placed when it is discussed— species, genus, family, class, as opposed to subgenus, subfamily, superfamily, etc.), should be conservative (Ehrlich and Murphy, 1983c) and the Lycaenidae retained as a single family. No thorough study recommending the elevation of any of the lycaenid subfamilies has, in fact, been published.

This, of course, has not prevented arbitrary taxonomic inflation among the butterflies by people who are unfamiliar with good taxonomic practice, the diversity of other groups, and the morphology, behavior, and/or the food plant relationships of the global butterfly fauna. In modern times, the most egregious treatment of butterfly families was probably that of Clark (1948) who, without giving the slightest justification, recognized 13 "families" within the Papilionoidea, including "Apaturidae" and "Argynnidae." More common errors include considering the "Heliconiidae" (e.g., Miller and Brown, 1981) as a family—even though *Argynnis* and *Heliconius* are connected by such clear intermediates that it is a toss-up whether or

not the latter should be separated from the tribe Argynnini of the Nymphalinae.

There is, also, the persistence of the "Satyridae" as a family (following Clark) in many publications on butterflies, even though its distinctness is an artifact of the temperate-zone bias of most lepidopterists. Indeed, the similarities between the Satyrinae and Morphinae are great enough that the Brassolinae were included in Morphinae by Ehrlich (1958b) and in "Satyridae" (distinct from "Morphidae") by Miller (1968), a circumstance underlining their subfamily status. In his major revision of the Satyrinae, Miller noted that "In neither paper did Clark [1947, 1948] give definitive reasons for his classification, hence he has been criticized by such authors as Ehrlich (1958)." Nonetheless, Miller perpetuated Clark's unsupportable classification and has persisted in doing so (Miller and Brown, 1983b).

Miller's (1968) revision of the Satyrinae, which could serve as a model of the sort of taxonomic analysis that is needed for virtually every other subfamily of butterflies, is thus flawed by a one-step nomenclatural inflation. Much the same might be said for Eliot's (1973) otherwise fine work on the Lycaenidae. Eliot defends his taxonomic treatment with "there are advantages in upgrading numerically large groups into families... since this facilitates their further subdivision using only generally accepted categories of subfamily, tribe, genus and subgenus." That unfortunate rationale applied to the family Tipulidae, the crane flies, which contains around 11,000-12,000 described species (about the same number as all of the butterflies) would force it to be split into several families. And what then should be done with various beetle families: the Tenebrionidae have more than 15,000 species, the Scarabidae 17,000, the Cerambycidae and Chrysomelidae 20,000 each (CSIRO, 1974)? The Curculionidae with its 60,000 species and some 75 subfamilies should be an order, or perhaps a class (remember that the classes Aves and Mammalia have just 8,200 and 4,500 species respectively [Ehrlich et al., 1976]). The key point is that it is important for taxonomies to reflect evolutionarily fascinating situations where swarms of closely similar forms exist without big gaps, not to disguise them by splitting.

Accepting Clark's raft of family names based on minor differences in superficial characters leads to such absurdities as recognizing the "superfamily" Lycaenoidea (e.g., most recently Ferris and Brown, 1981). Presuming that these authors would continue to recognize Lepidoptera as an order and would not propose many new suborders or infraorders, Ferris and Brown then ask us: 1) to consider nymphalid-tortricid differences or lycaenid-sphingid differences, or 2) to recognize on the order of 100 new lepidopteran superfamilies equivalent to Lycaenoidea and Nymphaloidea— e.g., Lasiocampoidea, Scythroidea, Uranoidea, Megathymoidea, etc.

That level of splitting can be compared to the mere 24 superfamilies in

the order Hymenoptera, a group much more diverse biologically than the Lepidoptera. One of those, the Apoidea, contains all of the bee families— honey bees, orchid bees, carpenter bees, sweat bees, bumble bees, and so on—with their diverse morphologies and social structures. Even so, the Apoidea might be considered just a segregant of convenience from the sphecoid wasps.

There are, in any case, more questions about the recognition of subfamilies in the butterflies than there are about the families. This is especially true within the Lycaenidae, and to a lesser extent, the Nymphalidae—both very species-rich groups. Large gaps do not appear to have been created either by divergence into unique habitats or by extinctions. Continuous patterns of variation make imposing hierarchical structure especially difficult as nature is "bent" to fit the formalities of the taxonomic system.

A classic example, mentioned above, involves *Heliconius* (Nymphalinae: Heliconiini), which are basically tropical fritillaries. They are connected to their Nearctic relatives in the genus *Speyeria* (Nymphalinae: Argynnini) by intermediate forms such as those in the genera *Euptoieta, Agraulis, Dione,* and *Dryas*. In spite of the continuum, the *Heliconius* show characteristics such as longevity and relatively complex behavior that make it wise, at least, to recognize them with tribal status rather than to submerge them in the Argynnini. If there were no intermediates between *Speyeria* and *Heliconius* and if the subgenus *Euides* did not exist within the *Heliconius*, a reasonable argument could be made for raising the genus to a monobasic subfamily Heliconiinae. This example demonstrates that, even when the degrees of extant relationships are rather well agreed upon, the solution to nomenclatural problems is far from automatic. Placement of *Heliconius* into a higher category depends not just upon its relationship to *Argynnis*, but also upon the gaps that extinction has or has not created between the two genera.

Unfortunately, the fascinating questions of the higher classification of the butterflies only rarely have been the subject of the careful investigations they deserve. The tradition of looking carefully at many characters over a broad sampling of butterflies, traceable as far back as Samuel Hubbard Scudder, has all too often been neglected in studies either too narrow in scope or based on relatively too few characteristics. (Scudder was also a rather extreme splitter, but good nomenclatural practice has evolved a great deal in the past century.)

Generic Level

Genera are, of course, collections of species. Since the generic name is the first part of the specific name, it is especially important that generic names be applied conservatively since changes greatly reduce the communication function of taxonomy (Ehrlich and Murphy, 1982, 1983a,

c). The rule of obligatory categories, therefore, is most important at this level. In North America, the generic nomenclature as expressed in standard works like Klots (1951), Ehrlich and Ehrlich (1961), dos Passos (1964), and Howe (1975) is probably somewhat oversplit but should be retained for purposes of stability. For example, for communicating with non-specialist scientists and laypersons, it might be better if *Speyeria* and *Argynnis* (along with palearctic *Mesoacidalia* and *Fabriciana*) had both been retained as subgenera of *Argynnis*, and *Chlosyne* and *Euphydryas* (along with *Mellicta*) as subgenera of *Melitaea*. But a more split nomenclature probably serves the purposes of specialists better, so the nomenclature of those standard works did not generate serious problems.

The *Palearctic* butterfly genera (Higgins, 1975) have been extremely oversplit, and this has spawned a similar mistreatment of Nearctic butterfly genera (Miller and Brown, 1981). This condition, happily, will be short-lived, following the appearance of appropriately conservative nomenclature in *Butterflies of Europe* by Kudrna, *Butterflies East of the Plains: an Illustrated Natural History* by Opler and Krizek, and *The Butterflies of North America: a Natural History and Field Guide* by Scott.

Taxonomic work at the generic level in butterflies, like that at higher taxonomic levels, demands a complete assessment of related species. For example, it is inadequate to set generic limits on, say, *Callophrys* and its relatives, without consideration of several dozen of the most distinct genera of hairstreaks as well as the tribal structure of the Lycaeninae. Studies not encompassing an examination of a wide range of morphological characters, patterns of food plant preference, and allozyme genetics, are probably insufficient for setting such limits.

The application of electrophoresis to measure heritable variations in enzymes and other proteins has tremendous, virtually untapped potential as a concomitant to more traditional systematic methods. Two features of electrophoresis make it unusually valuable for uncovering distorted balance in taxonomic studies. First, it is a comparatively objective means of assessing phenotypic differences that avoids the inherent problems of interpreting and weighting morphological characters. Second, genetic similarities are extremely high among populations of the same subspecies and, conversely, are incrementally lower among increasingly distantly related taxa (e.g., Avise, 1975).

Comparisons of phenon levels (the levels of differentiation at which various taxonomic ranks—subspecies, species, genus—are assigned) have been presented for the butterfly taxa for which the most extensive electrophoretic data exist (Brittnacher et al., 1978; Geiger, 1980; Brussard et al., 1984). These studies show unambiguously that recent treatments of Nearctic butterfly genera by Ferris and Brown (1981) and Miller and Brown (1981, 1983b) following the lead of Higgins (1975) use many badly oversplit genera. In particular, the recognition of generic status for

"*Occidryas,*" "*Hypodryas,*" and "*Artogeia*" and tribal status for "Euphyd-
rini" and "Euchloini" are shown to be unwarranted—something that was
apparent earlier on the basis of common sense.

Species Level

There is no more enduring controversy in taxonomy than that surrounding
the definition of species (see in this journal Shapiro, 1983; Ehrlich and
Murphy, 1983 b). The technicalities of the arguments cannot be dealt with
here, and it is unnecessary since, in practice, taxonomists usually agree on
what is or is not a species. Species are distinct *kinds* of organisms—they do
not normally interbreed with other kinds with which they are sympatric
(where they co-occur geographically), and they are normally separated by
clear morphological gaps from other allopatric species those occurring in
different geographic areas).

The most serious problem with species definitions comes when one
attempts to evaluate the degree of distinctness of allopatric entities. Are
Lycaena phlaeas and *Coenonympha tullia* in North America, for example, the
same species as *Lycaena phlaeas*, and *Coenonympha tullia* in Europe? Are
the Nearctic *Pieris occidentalis* and the Palearctic *P. callidice* actually
conspecific (Shapiro, 1976; Ehrlich and Murphy, 1983 b)?

Species level taxonomy should be based on as many characters as possible
and not, for example, purely on the morphology of the genitalia. To avoid
naming unwarranted regional "species" which may be mere intergradations
along a continuum of seemingly distinct, geographically distant populations
(a problem typified by recent species level descriptions in the *Mitoura*
[Johnson 1977; Brown, 1982]), species level taxonomy should, to the
greatest degree possible, be based on characters measured through entire
geographic ranges to identify clines among closely related taxa (e.g. Scott,
1980). Striking differences in the genitalia often do indicate separate specific
status, yet substantial genitalic variation can exist within some species
(Shapiro, 1978). *Euphydryas editha* and *E. chalcedona*, sibling species on
the basis of electrophoretic analysis, exemplify both conditions, Their male
genitalia are distinct, the two processes of the valval armature diverging by
an angle greater than 90° in *E. editha* and less than 90° in *E. chalcedona*
(Ehrlich and Ehrlich, 1961; Murphy and Ehrlich, 1984). Within *E. editha*
there is essentially no variation in process length among populations that
show extensive variation in wing patterns and ecological characteristics. *E.
chalcedona*, in contrast, shows dramatic intra- and interpopulation dif-
ferences in the length and curvature of the processes (Scott, 1978 a), and
overlaps in this character with some populations of *E. anicia* with which it
may be conspecific (Scott, 1978; Ehrlich and Murphy, 1983 b). Similar
situations exist in Nearctic *Euphilotes* and Palearctic *Pseudophilotes* and
Maculinea.

Such complexity within closely related groups of species is consistent with

the finding that valval length is controlled by a single gene (Turner et al., 1961). But, interestingly, we know of few cases of butterflies that are unambiguously specifically distinct which lack clear differences in the male genitalia, although the reason for this is not at all obvious. (Some exceptions include *Oenesis melissa, jutta* and *alpina excubitor; Callophrys sheridani, dumetorum viridis,* and *affinis perplexa*—J. A. Scott pers. comm.; *Glaucopsyche lygdamus* and *piasus*—R. H. T. Mattoni, pers. comm.; and the many *Polyommatus* blues, discussed below.) Female genitalia are much more frequently undifferentiated. For instance, we have been unable to determine any female genitalic character that flawlessly separates *Euphydryas editha* from *Euphydryas chalcedona,* although in some groups such as *Papilio glaucus* (Scott, 1976) and members of the genus *Erebia* (Ehrlich, 1952), differences in the female genitalia may be more striking than those in the male.

When working at the specific level, both crossing experiments (to determine levels of infertility) and allozyme studies can be particularly helpful in attempting to sort out problem complexes. However, it is already abundantly evident from our own work on *Euphydryas* as well as from investigations of other groups such as the *Papilio machaon* complex or *Papilio glaucus* vs. *P. rutulus*, the genus *Speyeria, Phyciodes* (Oliver, 1978) and so on, that in some cases unambiguous division of groups into distinct species with no questionable or borderline cases cannot be done now, and is unlikely to be done in the future.

This, of course, comes as no surprise to evolutionists. One would expect a continuous pattern of differentiation of populations, and a certain proportion of entities to be at an intermediate level of differentiation—on the path to becoming clearly distinct kinds but not yet there—at any given time. What proportion should be species *in statu nascendi* is still a matter of dispute among evolutionists, as the current "punctuated equilibrium" (e.g., Eldredge and Gould, 1972; Gould and Eldredge, 1977; Gould, 1980) vs. "gradualism" debate shows, but finding intermediate situations such as the Euphydryas chalcedona-anicia complex presents problems only for taxonomists trying to arrange specimens in insect collections, certainly not for evolutionary biologists.

Subspecies Level

Since the early 1950 s, and particularly since the seminal paper by Wilson and Brown (1953), it has been clear that most subspecies are not discrete entities of evolutionary significance. Rather, they are arbitrary geographical subdivisions of a species delimited by variation of one, a few, or many characters. Recognized subspecies are, for the most part, different depending on which characters are selected—for a classic example from the butterflies, see Gillham's (1956) analysis of North American *Coenonympha.*

The basic problem is that, in most species, character variation is

discordant. Characters tend to vary in patterns that are not closely related to one another—as one might expect due to (presumably) different selection pressures acting on them. Subspecies of butterflies, not surprisingly, often have been described solely on the basis of geographic variation in wing patterns and colors. Consequently, in many cases more or fewer subspecies might have been described had different characters been used. *Euphydryas* again provides an example. Populations of *E. chalcedona* west of the Sierra Nevada crest, from foothills to coast, locally feed as larvae on a single host plant species or combinations of host plant species in nearly a dozen genera in the Scrophulariaceae. They also show substantial variation in the male genitalia. Yet, since virtually all individuals have black and yellow dorsal wing markings, all have been lumped in *E. chalcedona chalcedona*. Along the east slope of the Sierra into the Great Basin, conversely, nearly all populations are monophagous on a single larval host plant and show less variation in male genitalia. However, since combinations of red, black, and yellow wing markings vary extensively, two species names (*E. chalcedona* and *E. anicia*) and a variety of subspecies names have been applied.

In some cases, however, character variation may be concordant, in which case the subspecies delineated may be real biological entities. Two cases in butterflies where this may be the situation are *Euphydryas editha* (Murphy, et al., in prep.) and, apparently, *Euphilotes. E. editha* appears to be divided into a number of ecotypes, each adapted to a different suite of environmental conditions, and each geographically isolated from other ecotypes. Not only are there phenetic differences between ecotypes, but evidence for concordant genetic differentiation in oviposition host plant choice (Singer, 1982), in both egg mass size and individual egg weight (Singer et al., in preparation), and in electrophoretically identifiable variation at some gene loci. Similar situations may occur in other butterflies, but the detailed studies of ecology and genetics required to elucidate them simply have not been done.

All this is not to say that the standard "A new subspecies of *Boloria eunomia* from Wyoming" kind of paper, naming the organisms from a geographic area and describing their differences from those in another geographic area, are without value. Although such subspecies are of little usefulness from an evolutionary or a biological point of view (in fact, they can disguise the real patterns of geographic variation), when afforded protection, subspecies may be of immense value in the conservation of species. Indeed, the critical thing is not just to preserve names, but to preserve the geographic and, hopefully, the genetic variability that is often essential to the persistence of species.

The Splitting Problem

As we have indicated (Ehrlich and Murphy, 1982, 1983a, c), the most pervasive problem in butterfly nomenclature is inflation of generic names,

the most disruptive consequence of which is the instability of latinized binomens. While published work on the higher taxonomy of butterflies can be ignored (and, in the case of the more thorough work, clearly often has been), taxonomy at the levels of genus and species directly affects the way scientists communicate. For this reason, taxonomic changes at these levels should be avoided whenever possible.

The recent wholesale abandonment of this "rule" originated in works on Palearctic butterflies (Higgins and Riley, 1970; Higgins, 1975), and, by and large, European genera have been fragmented without justification. But the mere application of names, justified or not, lends credence to them since users rarely have both access to pertinent works and the background to analyze them critically.

Consider Higgins' (1975) treatment of the blues he places in the tribe Polyommatini. Warning that wing characters are not particularly reliable above the species level (p. 9), Higgins then presents a key to sixteen "genera" of these blues (pp. 137-138) based largely on those characters. Another character separating genera in the very first couplet of the key is a hairy versus hairless condition of the eyes; this despite both conditions existing within the genus *Agrodiaetus*—an "anomaly" according to Higgins! But is this character state in *Agrodiaetus* really an anomaly, or is it indicative of the arbitrary splitting of a large group of very closely related species? The latter is indicated by the transfer without explanation of *amanda, escheri,* and *thersites* between *Plebicula* (Higgins and Riley, 1970) and *Agrodiaetus* (Higgins, 1975). Those two "genera", lacking distinguishable genitalia, are separated by the presence or absence of a single white wing marking. And, despite a range in chromosome number between 22 and 223 among species assigned to these two groups, those with less than 125 are assigned to *Agrodiaetus* and more than 134 to *Plebicula* (Higgins, 1975). Eliot and Kawazoe (1983) comment that a treatment of this group in balance with their classification of *Lycaenopsis* would necessitate sinking "*Lysandra, Plebicula, Agrodiaetus,* and *Meleageria* (all in common European usage) and possibly some other genera as subjective synonyms of *Polyommatus*, while *Polyommatus* itself would become a subgenus of *Plebejus*."

Clearly, Higgins' (1975) treatment has obscured rather than elucidated relationships among species in this biologically interesting group. Why then split up apparently cohesive genera? The answer seems to lie elsewhere in the book. Referring to *Erebia* (p. 223) Higgins writes, "the forty-five species recognized in this book are placed in a single genus; all are so closely related that attempts at generic division have not been successful." We suggest that attempts at generic division have been equally unsuccessful in *Polyommatus, Lycaena, Argynnis, Melitaea, Pieris,* and others as well.

Epitomizing similar recent problems in Nearctic nomenclature is the case of so-called " Chalceria ferrisi", known to nearly all lepidopterists as

Lycaena rubidus. Johnson and Balogh (1977), in a veritable epic (sixty-two page!) assault on "the *Lycaena rubidus* complex", erected a sibling species *L. ferrisi* because (p. 42) it is "obviously reproductively isolated in nature", has genitalia divergent to the same degree as species *L. xanthoides* and *editha*, and some differing wing characters. Johnson and Balogh confuse reproductive isolation, which they did not test, with geographic isolation. If geographic isolation were the standard for specific distinctions, then Indian and African lions would be different species, and there would be dozens of "species" within what is now called *Euphydryas editha, Papilio indra, Speyeria nokomis,* etc. And, Scott (1980) has since established that introgression occurs between *xanthoides* and *editha,* that the wing characters are variable in *ferrisi* populations, and that *rubidus* and *ferrisi* should be considered conspecific.

Miller and Brown (1979) contend that *Lycaena* is simply too diverse to retain as a genus, resurrecting two long-ignored genera, "Gaeides" for *xanthoides, editha,* and *gorgon,* and "Chalceria" for *rubidus, "ferrisi"* and *heteronea.* Noting that "*gorgon*. . .does not entirely fit *Gaeides*", in fact "tends to unite *Gaeides* and *Chalceria*", they nonetheless conclude that "considering the two genera separate, though closely related, seems best." Closely related? They certainly are. Scott (1980) documents several "Gaeides" x "Chalceria" hybrids and indicates that the genitalia of *Lycaena xanthoides* and *L. rubidus* are virtually identical.

But Miller and Brown (1979) go further, erecting a mythical "possible phylognetic chart" for the nearctic "Lycaeninae" (that is, of course, the genus *Lycaena*), adding (p. 25) "all of this is guesswork, but it is educated guesswork. It is what we currently think." What they currently think includes the separation of these still hybridizing "genera" some 50 million years ago. (Gorillas, chimpanzees, and human beings had a common ancestor less than 20 million years ago!) Sufficient time was obviously available for the divergence of yet another "genus", this one monotypic, "Hyllolycaena", which among other things has a ventral wing surface pattern "almost identical" to *xanthoides dione* and genitalia inseparable from *heteronea.* These coppers were treated by dos Passos (1964) as six species with ten described subspecies in a single genus. Miller and Brown (1981, 1983), despite evidence favoring reduction of that to five species, give us instead seven species with twelve subspecies (four new) in three genera.

The *Lycaena* mess seems to reflect the misapprehension that the presence of distinct species groups within a genus mandates its splitting. Because *Papilio rutulus* and *P. multicaudatus* are more similar to one another than either is to *P. machaon* is not adequate reason for splitting the former off as *Pterourus* (Miller and Brown, 1981 and, now, Hancock, 1983), nor would splitting up the subgenus *Pterourus* because the former two are more similar to each other than either is to *Papilio (Pterourus)*

homerus. Certainly, anyone familiar with intraspecific variation in butter-
flies can appreciate the absurdity of "generic" differentiation represented
by this couplet from Hancock (1983, p. 31):

3   Pattern primitive-banded or dark with pale bands and spots;
       clasper narrow, ventral, with a dorso-apical serrate plate;
       mature larva green, white or pink with segmental black bands
       and yellow, orange, pink or red spots and no metathoracic eye-
       spots. . . . . . . *Papilio* Linnaeus (part)

—   Pattern primitive-banded or dark with pale bands and spots or
       mimetic of *Battus* or Ithomiinae; clasper broad or narrow,
       apically spiny or dentate; mature larva green with a brown X-
       shaped abdominal saddle or blue or purple segmental spots;
       metathoracic eye-spots present. . . . . . . *Pterourus* Scopoli. 4

Two of the above mentioned sources have explained their preferences
for fractionated genera with opposing arguments. Miller and Brown
(1983a) convolutedly contend that varying rates of evolution between
butterfly groups has resulted in certain groups having "better" (read
"more", apparently) genera than others. Hancock (1983), on the other
hand, attempts "to correlate genera with an evolutionary time scale" and,
despite the wholly arbitrary nature of his time scale, splits genera in one
tribe to "parallel" another "where distinct genera are recognizable."

As we have pointed out (Ehrlich and Murphy, 1983a), historical rates of
evolution, even if they were ascertainable (which almost always, in such
groups as butterflies with negligible fossil records, they are not), make no
difference whatsoever in the application of a sensible nomenclature.
Furthermore, what these "phylogenetic" treatments (including that of
Miller and Brown, 1981) have in common is that they do not consider
balance within the Lepidoptera, much less within the insects. Perhaps
worst of all, they share a reliance on intuition for their basic organization
and for determining taxon lines. Hancock (1983) explains his new
treatment of papilionids with "it is felt that such an arrangement is the
most natural and logical attainable at the present time." Yet these
subjectively justified new taxonomies are praised by some lepidopterists
(e.g., Ferris, 1984). Sadly, Sokal and Sneath's (1963) statement, "Un-
doubtedly more utter rubbish has been written. . .on supposed phylogenies
than on any other biological topic," remains as pertinent as ever.

It is appropriate here to compare the overall diversity of butterflies to
their lepidopteran relatives (Table 1). While the four other superfamilies
have far more North American species than the butterflies, butterflies are
the most taxonomically subdivided with many fewer species per genus
than these representative moth groups. Certainly, it is not legitimate
to argue that butterflies are more diverse ecologically. Not only have
moths of many superfamilies successfully invaded both diurnal and

TABLE 1

	Papilionoidea	Geometroidea	Noctuoidae	Gelechioidea	Tortricoidea
Species	470	1414	3358	1460	1164
No. of families	9	4	5	9	2
No. of subfamilies	26	9	25	24	4
species/family	52.2	353.5	671.6	162.2	582.0
species/subfamily	18.1	157.1	134.3	60.8	291.0
genera	147	260	735	203	100
genera/family	16.3	65.0	147	22.6	50
genera/subfamily	5.7	28.9	29.4	8.5	25
species/genus	3.2	5.5	4.6	7.2	11.6
pages	17	19	47.5	14	11.3
species/page	28	74.4	76.9	104	103

Table 1. Constructed from Hodges et al., 1983.

nocturnal "niches", but the Gelechioidea (the moth superfamily among these shown which has overall taxonomic statistics most similar to the butterflies) is immensely more diversified ecologically, and includes leaf miners, case bearers, borers, gall makers, and scavengers, as well as external foliage feeders (Powell, 1980). Perhaps most telling is the number of *species per page* in the Hodges, et al. checklist; about one-third as many butterfly names appear per page, due both to the bloated, over-fractionated hierarchy and to the hordes of name changes and synonymies.

Why do Taxonomic work on Butterflies?

There are estimated to be between 5 to 30 million different species of organisms, most of them insects. Well under two million have been named and only a bare handful have had any significant work on their genetics (some *Drosophila, Colias, Mus, Zea, Escherichia coli, Neurospora,* etc.) or ecology (red deer, Caribbean anoles, intertidal invertebrates, *Achillea, Euphydryas editha,* etc.). It is clear that, even if *Homo sapiens* were not busily destroying the diversity on this planet, most organisms would go extinct or evolve into something else before there would be an opportunity to study them at the level of today's few "well-known" plants and animals (when for those, in most cases, the surface has barely been scratched). There is no hope of ever "completing the job" (Ehrlich, 1964).

What is badly needed is a sampling approach to nature in which most

systematic effort goes into a relatively few representative groups on which a reasonable start has already been made, or for which there appears to be some unique attribute that makes them especially worthy of study. Among the insects, the butterflies, yucca moths, fruit flies, and the social insects are examples of four such groups. There are probably only about fifteen thousand butterfly species, so that the task of completing their alpha taxonomy (description of species) in all stages and their beta taxonomy (arranging those species in higher categories) is already well advanced and could be completed with a few decades of intensive work.

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An Annotated Catalogue of the Skippers (Lepidoptera: Hesperiidae) named by Roger Verity

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Abstract. Species-group and infrasubspecific taxa of the family Hesperiidae named by R. Verity (1883-1959) are listed, with bibliographical data, information on their type-material, and notes on their taxanomic status and/or identity. Proposals are made with regard to the stabilization of their nomenclature.

Apart from over 1500 butterflies (Papilionoidea), R. Verity (1883-1959) named 136 species-group and infrasubspecific taxa of Palaearctic skippers (Hesperiidae), and probably no fewer taxa of the family Zygaenidae. The aim of the present paper is to provide the student of the family Hesperiidae with an annotated catalogue of Palaearctic skippers named by R. Verity, it being continuation of a similar catalogue of the butterflies (Kudrna, 1983). It is hoped that this paper will contribute to the stabilization of nomenclature and provide basic taxonomic data for further study. The paper is based on the study of Verity's publications, examination of type-material deposited at the Museo Zoologico de la Specola in Florence and other relevant papers concerning the subject. It is hoped to conclude the project with a catalogue of Zygaenidae in the forseeable future.

Whatever has been said in the introduction to the catalogue of butterflies (Kudrna, 1983), is applicable to the Hesperiidae, as well as certain information published earlier (Kudrna, 1976, 1982). Thus the inclusion of a general introduction regarding Verity's life, work and taxonomic concepts is unnecessary. Verity's publications concerning only Hesperiidae were not included in his annotated bibliography (Kudrna, 1983), but listed by both Baccetti (1963) and Beer (1960); they are also cited here (cf. literature cited); papers already listed by Kudrna (1983) are not repeated.

All names are arranged in alphabetical order, each entry consisting of: caption (abbreviated original rank)—original combination author, year—

bibliographical reference—type-material (if found) or type-locality (if known) or relevant information—comments and/or taxonomic history. Original taxonomic categories are abbreviated as follows: sp = species, ssp = subspecies, ra = race, sf = seasonal form, if = individual/infrasubspecific form, aberration, sr = subrace, nn = nomen novum (nomen nudum is never abbreviated), ? = category uncertain. Caption is printed (1) in capitals for names originally intended for species-group taxa (i.e. species, subspecies and their replacement names); (2) in lower case preceded by asterisk for trinominal Verity's "race" recommended (Kudrna, 1983) for subspecies-rank (for the sake of stabilization of nomenclature); and (3) in lower case without asterisk for infrasubspecific taxa. Detailed discussion of Verity's taxonomic categories and reasons for the above treatment have already been given elsewhere (Kudrna, 1982, 1983). The International Commission on Zoological Nomenclature should make use of its plenary powers for settling of subjective opinions regarding Verity's names as outlined by Kudrna (1983).

All type-material listed is deposited in Museo Zoologico de la Specolà, Via Romana 17, I-50125 Firenze, Italy. The problems concerning the type-material extracted from glass cases were discussed by Kudrna (1983). As in the earlier work (Kudrna, 1983) all data concerning type-material were taken directly from specimen labels. Parts placed in square brackets are our additons supplementing incomplete data, occasional additional comments in parenthesis concerns only the interpretation of geographical names. All users of this catalogue are strongly advised to study first the general parts of the butterfly catalogue (Kudrna, 1983).

Evans (1949) overlooked a number of skippers named by R. Verity, and of those known to him, he sunk as synonyms all but six taxa treated as subspecies; references to these are given elsewhere in this catalogue. Evans (1949:343) erroneously attributed to Verity the authorship of *Thymelicus sylvestris obscura*, dated 1905, and treated as a subspecies; the name was originally proposed for an aberration *Adopaea flava obscura* Tutt, 1905 and is not available.

*accreta (ra)—*Hesperia alveus accreta* Verity, 1925—Entomologist's Rec. J. Var. .37:55—Syntypes 8♂♂ [France]: H[autes]-P[yrenees]: Gedre: VII [19]16: Rondou [leg.]—Warren (1926): *Hesperia alveus accreta* (ssp.); Jong (1972): *Pyrgus alveus accretus* (ssp.); First raised to species-rank by Warren (1953) and recently confirmed by Balletto, Cassulo & Toso (1983).

aegra (sf)—*Erynnis marrubii aegra* Verity, 1925—Entomologist's Rec. J. Var. 37:42—Syntype(?) 1♂ [France: Marseille]—Status and origin uncertain.

*__albens__ (ra)—*Hesperia ryffelensis albens* Verity, 1925—Entomologist's Rec.J.Var. 37:56—Syntype 1♂ [Czechoslovakia]: Mahren (= Moravia): Olmutz (= Olomouc)— Possibly described from a single specimen: holotype by implication—Warren (1926): synonym of *Hesperia alveus scandinavicus* Strand, 1903.

albodetersa (if)—*Powellia sertorius albodetersa* Verity, 1929—Mus. barcin. Scient. nat. Op. 11(4):17—(?)Holotype ♂ [N. Italy: Alpi Marittime: Terme di] Valdieri: [1375 m]: 26 VII [19]09: [Verity leg.]; *albodetersa.*

alboinspersa (if)—*Hesperia malvoides pseudomalvae alboinspersa* Verity, 1916— Boll. Soc. ent. ital. 47(1915):65—Italy: provincia di Macerata (by implication).

albovelata (if)—*Hesperia onopordi albovelata* Verity, 1919—Entomologist's Rec. J. Var. 31:27—(?)Italy: Florence.

*__alioides__ (ra)—*Powellia sao alioides* Verity, 1926—Entomologist's Rec. J. Var. 38:103—Syntypes 9♂♂, 2♀♀ [N. Italy]: Alpi Cozie: Val Susa: Oulx: 1100 m: 4 VII-12 VIII 1925: Verity [leg.]—Jong (1974): *Spialia sertorius sertorius alioides* (infrasub-specific form).

*__alpapennina__(ra)—*Urbicola comma alpapennina* Verity, 1928—Bull. Soc. ent. Fr. 1928:125—Syntypes 9♂♂, 5♀♀ Italia centrale: Macerata: Monti Sibillini: Bolognola: 1200 m: 13 VIII-8 IX 1919: Querci [leg.].

alpestris (nn)—*Pyrgus malvae malvoides alpestris* Verity, 1940—Le farfalle diurne d'Italia 1:42—Replacement name proposed in a quadrinominal original combina-tion for "var[iety]" *Hesperia malvae alpina* Tutt, 1906, treated as "razza?", and said to be primary junior homonym of *Hesperia alpina* Erschoff, 1874, which was recognized as a distinct species by both Warren (1926) and Jong (1972). Warren (1926) treated Tutt's name *alpina* as a junior subjective synonym of *Hesperia malvoides* Elwes & Edwards, 1898, and Jong (1972) probably overlooked or excluded by implication both Tutt's and Verity's above mentioned names.

*__alpiumflava__ (ra)—*Urbicola comma alpiumflava* Verity, 1928—Bull. Soc. ent. Fr. 1928:126—Syntypes 4♂♂, 1♀ Italia settentrionale: Alto Adige: [Bolzano]: Colle: 1000 m, Valle Isarco: Campodazo: 23-30 VII [19]20: Kollar [leg.]—None of the specimens bears complete data on its label.

*__ambigua__ (ra)—*Erynnis stauderi ambigua* Verity, 1925—Entomologist's Rec. J. Var. 37:43—Syria: Akbes—Name for a specimen figured by Oberthür (1911) in Etud. Lepid. comp. 5:pl. LXIV, fig. 607—Evans (1949): *Carcharodus stauderi ambigua* (ssp.).

*__asiaeclara__ (ra)—*Syrichtus malvae asiaeclara* Verity, 1934—Entomologist's Rec. J. Var. 46:(7)—Syntypes 4♂♂ Chines. Turkestan: Tianchan mont. or.: Juldus Tal: 2500 m: Juli: [ex O. Bang-Haas].

*__atralpina__ (ra)—*Urbicola comma atralpina* Verity, 1929—Bull. Soc. ent. Fr. 1928:127—Syntypes 5♂♂, 2♀♀ [N. Italy]: Alpi Retiche: Stelvio: III Cant[oniera]: 10 VIII [19]27; Sulden-Ortler: 1800 m: 3-10 VII [19]20: (all) Verity [leg.].

*__atrata__ (ra)—*Hesperia carlinae atrata* Verity, 1925—Entomologist's Rec. J. Var. 37:57—Syntypes 11♂♂ [N. Italy: Piemonte]: Val Formazza: [Frua Waterfall]: 1400

m: 4 VIII [19]24: Verity [leg.]—Warren (1926): synonym of *Hesperia carlinae* Rambur, 1842; Jong (1972): sunk by implication and not unequivocally (cline) as a synonym of *Pyrgus carlinae* Rambur, 1839.

*****aurata** (ra)—*Urbicola comma aurata* Verity, 1924—Entomologist's Rec. J. Var. 36:107—Syntypes 3♂♂, 3♀♀ [Italy: Toscana: Appennino Pistoiese]: Abetone [Pass: 1300 m: Verity leg.].

aurescens (if)—*Thymelicus acteon aurescens* Verity, 1940—Le farfalle diurne d'Italia 1:104—Replacement name proposed conditionally for aberration *Thymelicus acteon clara* Tutt, 1905, deemed necessary if elevated to the rank of race and treated in the genus *Adopoea* Billberg, 1820 (i.e. conditional secondary homonymy of an unavailable infrasubspecific name).

*****australiformis** (ra)—*Erynnis altheae australiformis* Verity, 1919—Entomologist's Rec. J. Var. 31:27—Syntypes 2♂♂ Italia centrale: Toscana: Firenze: Pian di Mugnone: 200 m: 8 VIII 1916, 6 IX 1917: Querci [leg.]—Warren (1926): *Spilothyrus altheae australiformis* (ssp.).

*****australior** (ra)—*Erynnis lavatherae australior* Verity, 1919—Entomologist's Rec. J. Var. 31:27—Syntypes 2♂♂, 1♀ Italia centrale: Toscana: Firenze: Colline di Firenze: 400 m: 27 VI [19]08, 18-26 VII 1914: Verity, Querci [leg.]—Warren (1926): *Carcharodus lavatherae australior* (ssp.).

*****australissima** (ra)—*Erynnis lavatherae australissima* Verity, 1925—Entomologist's Rec. J. Var. 37:41—Algeria: Sebdou, Lambese—Name for specimens figured by Oberthür (1911) in Etud. Lepid. comp. 5:pl. XLVI, fig. 603, 604—Warren (1926): synonym of *Carcharodus lavatherae rufescens* Oberthür, 1911.

autumnalis (sf)—*Reverdinus alchymillae australiformis autumnalis* Verity, 1940—Le farfalle diurne d'Italia 1:21—C. Italy: Toscana: Firenze.

bellieriformis (if)—*Pyrgus alveus bellieriformis* Verity, 1928—Bull. Soc. ent. Fr. 1928:141—Holotype ♂ [N. Italy]: Sulden-Ortler: 1800 m: 3-10 VIII [19]20: Verity [leg.]; type: *bellieriformis.*

cacaotica (if)—*Hesperia armoricanus cacaotica* Verity, 1929—Mus. barcin. Scient. nat. Op. 11(4):15—Holotype ♂ Italia centr[ale: Toscana]: Lucca: Valle Camaione: 3-8 VI 1923: Querci [leg.]; type: *cacaotica*—Treated as (and probably raised to) a subspecies by Kauffmann (1951): *Pyrgus armoricanus cacaoticus* [nec Verity].

centralhispaniae (if)—*Hesperia alveus cetralhispaniae* Verity, 1925—Entomologist's Rec. J. Var. 37:55—Syntype 1♂ [Spain]: Aragon: [Prov. Teruel]: Albarracin: 1100 m: 10 VI [19]24: Querci [leg.]—Warren (1926): *Hesperia alveus centralhispaniae* [nec Verity] (ssp.); Jong (1972): *Pyrgus alveus centralhispaniae* (ssp.)—The name was probably raised to species-group status by Warren (1926), who must then take the authorship of the subspecies-rank name.

*****centralitaliae** (ra)—*Hesperia alveus centralitaliae* Verity, 1920—Entomologist's Rec. J. Var. 32:4—Syntypes 2♂♂, 1♀ Italia centrale: Piceno: Monti Sibillini: 1200-1400 m: 2 VIII-4 IX 1913; there are further 9♂♂ and 2♀♀ from the same locality which may possibly belong to the type-series—Warren (1926): *Hesperia alveus centralitaliae* (ssp.); Evans (1949): *Pyrgus alveus centralitaliae* (ssp.); Jong (1972): *Pyrgus alveus centralitaliae* (ssp.).

*claralveus (ra)—*Syrichtus alveus claralveus* Verity, 1934—Entomologist's Rec. J. Var. 46:(11)—Syntypes 7♂♂, 3♀♀ [N. Italy: Piemonte]: Alpi Cozie: Cesana Torin[ese]: 1300 m: 11 VII-1 VIII 1925: Verity [leg.].

claramaritima (?)—*Carcharodus fritillarius claramaritima* Verity, 1937—Entomologist's Rec. J. Var. 49:(2)—Turkey: Malatia: Tecde—Original rank uncertain: race or form.

*claraustralis (ra)—*Carcharodus fritillarius claraustralis* Verity, 1937—Entomologist's Rec. J. Var. 49:(2)—Syntypes(?) 2♂♂, 1♀ [Transjordania: Mt. Carmel: 4 VII ????]—Specimens unlabelled except for the name in Verity's handwriting under the first specimen; status uncertain, data by implication.

*elegantior (ra)—*Syrichtus malvae elegantior* Verity, 1934—Entomologist's Rec. J. Var. 46:(6)—Switzerland: Wallis: Upper Rhone valley: Martigny, Bex and/or other localities, all specimens collected by Wulfschlegel, now possibly lost—Jong (1972): *Pyrgus malvae malvae elegantior* treated as a possible "ecophenotypic" variation.

enervata (if)—*Hesperia armoricanus fulvoinspersa enervata* Verity, 1920—Boll. Lab. Zool. gen. agr. R. Scuola Agric. Portici 14:42—Italy: Campania: Caserta: Massiccio delle Mainarde—Warren (1926): *Hesperia armoricanus reverdini enervata* (ab.).

eschata (sf)—*Pyrgus armoricanus fulvoinspersa eschata* Verity, 1940—Le farfalle diurne d'Italia 1:70—Syntypes 4♂♂ Italia centrale: Toscana: Firenze: Pian di M[ugnone], Colline di Firenze: 200 m: Querci, [Verity leg.].

ESPERI (nn)—*Ochlodes venata esperi* Verity, 1934—Entomologist's Rec. J. Var. 46:(13)—Replacement name for *Papilio sylvanus* Esper, 1779 said to be a primary junior homonym of *Papilio sylvanus* Drury, 1773; the name was proposed as an available name of species-group status but was subjectively unnecessary because *Hesperia venata* Bremer & Grey, 1852, was available for the taxon.

exigua (if)—*Carcharodus alceae magnaustralis exigua* Verity, 1940—Le farfalle diurne d'Italia 1:14—Syntypes 1♂, 1♀ [C. Italy]: Lazio: Atina: 1-2 IX [19]38: Querci [leg.].

foulquieriformis (if)—*Hesperia alveus foulquieriformis* Verity, 1920—Entomologist's Rec. J. Var. 32:4—Holotype ♂ It[alia] c[entrale]: Piceno: Monti Sibillini: Dintorni Bolognola: 1200 m: VIII 1912—Described from a single specimen.

*fragilis (ra)—*Hesperia serratulae fragilis* Verity, 1925—Entomologist's Rec. J. Var. 37:56—Syntypes 3♂♂ Austria inf[erior]: Wien Umg[ebung]: Baden: VI 1924, VII 1924: Coll. Kollar—Data incomplete and poorly legible; treated as aberration by Warren (1926).

fulva (sf, ra)—*Erynnis marrubii fulva* (Verity, 1925—Entomologist's Re. J. Var. 37:43—Spain: Cuenca(?)—Name proposed for seasonal form of second generation and possibly (by implication) for a local race; data incomplete and uncertain; treated as a synonym of *Spilothyrus baeticus* Rambur, 1839, by Warren (1926).

fulvescens (sf, ra)— *Erynnis marrubii fulvescens* Verity, 1925—Entomologist's Rec. J. Var. 37:42—Syntypes(?) 1♂, 1♀ [S. France: Marseille]; origin and status of specimens uncertain—Treated as synonym of *Spilothyrus baeticus* Rambur, 1839,

by Warren (1926).

fulvipinnulis (sf)—*Erynnis altheae fulvipinnulis* Verity, 1924—Entomologist's Rec. J. Var. 36:106—C. Italy: Toscana.

fulvissima (sf)—*Erynnis stauderi fulvissima* Verity, 1925—Entomologist's Rec. J. Var. 37:44—Algeria—Warren (1926): infrasubspecific race of *Spilothyrus stauderi* Reverdin, 1913.

fulvocarens (if)—*Erynnis alceae fulvocarens* Verity, 1925—Entomologist's Rec. J. Var. 37:54—Holotype ♀ Italia centr[ale]: Ascoli Piceno: [Monti Sibillini]: Pizzo Tre Vescovi: [Tenna Valley]: 1200 m: 12 VII 1923: Querci [leg.].

fulvoinspersa (sf)—*Hesperia armoricanus fulvoinspersa* Verity, 1919—Entomologist's Rec. J. Var. 31:27—C. Italy: Toscana; proposed for the majority of specimens of second generation—Treated as an infrasubspecific race by Warren (1926) and sunk (by implication) as a synonym of *Pyrgus armoricanus armoricanus* Oberthür, 1910, by Jong (1972).

*****fulvosatura** (ra)—*Muschampia proto fulvosatura* Verity, 1925—Entomologist's Rec. J. Var. 37:54—[U.S.S.R. or Turkey]: Armenia—Warren (1926): aberration of *Sloperia proto* Ochsenheimer, 1808; Evans (1949): *Muschampia proto fulvosatura* (ssp.).

fulvotincta (sf)—*Hesperia onopordi fulvotincta* Verit, 1919—Entomologist's Rec. J. Var. 31:27—C. Italy: Toscana: Firenze—Treated as infrasubspecific race of *Hesperia onopordi* Rambur, 1839, by Warren (1926).

*****galliaemeridiei** (ra)—*Urbicola comma galliaemeridiei* Verity, 1928—Bull. Soc. ent. Fr. 1928:124—Syntypes 7♂♂, 1♀ [France: Hautes-Pyrenees]: Gedre: 24 VII [19]18, VII [19]24: Rondou [leg.]; most of syntypes have incomplete data labels, lacking the date of capture and collector's name.

*****gigas** (ra)—*Muschampia proto gigas* Verity, 1925—Entomologist's Rec. J. Var. 37:55—Morocco: Azrou—Warren (1926): infrasubspecific race of *Sloperia proto* Ochsenheimer, 1808.

gracilis (sf)—*Powellia sao gracilis* Verity, 1919—Entomologist's Rec. J. Var. 31:28—Syntypes 5♂♂, 1♀ C. Italy: Toscana: Firenze; all specimens ex glass case, remounted and relabelled—Warren (1926): *Powellia sertorius gracilis*, infrasubspecific race; Jong (1972); *Spialia sertorius sertorius gracilis*, form.

*****grandis** (ra)—*Hesperia alveus grandis* Verity, 1925—Entomologist's Rec. J. Var. 37:55—S. France: Alpes-Maritimes: St. Martin Vesubie; name for specimens illustrated by Oberthür (1913) in Etud. Lepid. comp. 8: pl. CXCIII, fig. 1877, 1878—Jong(1972): large form (and synonym by implication) of *Pyrgus alveus accretus* Verity, 1925.

grisea (sf)—*Erynnis marrubii grisea* Verity, 1925—Entomologist's Rec. J. Var. 37:42—Syntype 1♂ [S. France]: Marseille: 7 VI 1918—Warren (1926): aberration of *Spilothyrus baeticus* Rambur, 1829.

griseofulva (sf)—*Erynnis alceae griseofulva* Verity, 1924—Entomologist's Rec. J. Var. 36:106—Syntypes 8♂♂, 2♀♀ Italia centrale: Toscana: Firenze: Pian di Mugnone: 200 m: 15 VIII-27 IX 1917: Querci [leg.]—Warren (1926): synonym of *Erynnis alceae australis* Zeller, 1847.

*hemipallida (ra)—*Hesperia comma hemipallida* Verity, 1940—Le farfalle diurne d'Italia 1:116—Syntypes 3♂♂, 2♀♀ [Italy]: Sicilia: Madonie: VII; two specimens lack labels, data by implication only.

*hibera (ra)—*Urbicola comma hibera* Verity, 1928—Bull. Soc. ent. Fr. 1928:125— Syntypes 1♂, 1♀ [Spain]: Aragon: [Prov. Teruel]: Albarracin: 1100 m: 2 VIII & 1 IX [19]24: Querci [leg.].

*indicafusca (ra)—*Urbicola comma indicafusca* Verity, 1931—Bull. Soc. ent. Fr. 1931:200—Syntypes 8♂♂, 1♀ India sept[entrionalis]: Bashahr: [ex O. Bang-Haas]; five specimens without labels, data by implication.

infraflava (if)—*Augiades sylvanus sylvanus infraflava* Verity, 1920—Boll. Lab. Zool. gen. agr. R. Scuola Agric. Portici 14:45—C. Italy: Caserta: Massiccio delle Mainarde.

infralba (if)—*Carterocephalus palaemon infralba* Verity, 1940—Le farfalle diurne d'Italia 1:91—Holotype(?) ♂ Austria inferior: Klosterneub[urg]; status of specimen uncertain, locality given in publication does not agree with the specimen label.

infranigrans (if)—*Augiades sylvanus sylvanus infranigrans* Verity, 1920—Boll. Lab. Zool. gen. agr. R. Scuola Agric. Portici 14:45—Holotype ♂ Sud Italia: Caserta: Massiccio delle Mainarde: Valle Mollarino: 500 m: 7 VII 1919: Querci [leg.]; type: *infranigrans.*

*infraobscurata (ra)—*Pyrgus serratulae infraobscurata* Verity, 1938—Entomologist's Rec. J. Var. 50:(3)—Syntypes 4♂♂, 2♀♀ [N. Greece]: Macedonia: Olympus: [Skala]: 300 m: 16 & 18 VI 1935, 2-21 VII 1936: Romei [leg.].

infraochracea (if)—*Augiades sylvanus sylvanus infraochracea* Verity, 1920—Boll. Lab. Zool. gen. agr. R. Scuola Agric. Portici 14:45—S. Italy: Caserta: Massiccio delle Mainarde.

infraurata (if)—*Powellia sertorius infraurata* Verity, 1929—Mus. barcin. Scient. nat. Op. 11(4):16—Syntypes 8♂♂, 3♀♀ C. Italy: Toscana: Firenze: M. Fanna: 650 m: V [????]; all specimens ex glass case, remounted and relabelled; four from the original series of 15 specimens destroyed by museum pests.

infraviridis (if)—*Ochlodes venata infraviridis* Verity, 1940—Le farfalle diurne d'Italia 1:109—Holotype ♂ [Italy]: Abruzzo: Gran Sasso: 1300-1500 m: 28 VII 1939: Romei [leg.].

INSIGNIAMISCENS (ssp)—*Hesperia alveus insigniamiscens* Verity, 1929— Mus. barcin. Scient. nat. Op. 11(4):14—S. Spain: Sierra Nevada; names for specimens illustrated by Oberthür (1910) in Etud. Lepid. comp. 4: LV & CCXCV, fig. 2424 (holotype ♂) and 2431; name proposed originally as "nom. nov." which can be interpreted as implication of subspecies-rank—Jong (1972): *Pyrgus alveus insigniamiscens* (ssp.).

intermediaclara (sr)—*Adopoea lineola intermedia intermediaclara* Verity, 1940— Le farfalle diurne d'Italia 1:98—Syntypes 3♂♂ [N. Italy]: Alpi Retiche: Bormio: [1200 m]: 11 VII 1927: Verity [leg.]; name originally published hyphenated.

intermedialineola (sr)—*Adopoea lineola intermedia intermedialineola* Verity, 1940—Le farfalle diurne d'Italia 1:98—Syntypes 6♂♂ [N. Italy]: Alpi Pennine:

[Valle Anzasca]: Vanzone: 700 m: 5-12 VII [19]24: [Verity leg.]; name originally published hyphenated.

*italamixta (ra)—*Adopoea lineola italamixta* Verity, 1940—Le farfalle diurne d'Italia 1:96—Syntypes 2♂♂ Italia centrale: Toscana: [Firenze]: Sesto Fiorentino: 18 I 1917: Verity [leg.].

latealba (if)—*Hesperia serratulae latealba* Verity, 1925—Entomologist's Rec. J. Var. 37:56—Name for a specimen from Switzerland: Bernese Oberland, illustrated by Reverdin (1912) in Bull. Soc. Lepid. Geneve 2: pl. 4, fig. 6; treated as synonym of *Hesperia serratulae* Rambur, 1842, by Warren (1926).

lategrisea (if)—*Adopoea flava iberica lategrisea* Verity, 1920—Boll. Lab. Zool. gen. agr. R. Scuola Agric. Portici 14:43—S. Italy: Caserta: Massiccio delle Mainarde.

latenigra (if)—*Adopoea flava iberica latenigra* Verity, 1920—Boll. Lab. Zool. gen. agr. R. Scuola Agric. Portici 14:43—Holotype ♂ Sud Italia: [Caserta]: Massiccio delle Mainarde: Valle Mollarino: 500 m: 4 VII 1919: Querci [leg.]; type: *latenigra*.

LECERFI (nn)—*Hesperia armoricanus lecerfi* Verity, 1928—Bull. Soc. ent. Fr. 1928:140—Replacement name for *Hesperia armoricanus reverdini* Le Cerf, 1914, said to be preoccupied by *Hesperia alveus reverdini* Oberthur, 1912—Sunk (by implication) as a junior subjective synonym of *Pyrgus armoricanus persicus* Reverdin, 1913 (Jong, 1972).

luctuata (if)—*Hesperia malvoides luctuata* Verity, 1914—Boll. Soc. ent. ital. 45(1913):233—Italy: Toscana: Firenze.

*macrocomma (ra)—*Urbicola comma macrocomma* Verity, 1928—Bull. Soc. ent. Fr. 1928:126—Syntypes 9♂♂, 8♀♀ [N. Italy: Piemonte]: Alpi Cozie: Val Susa: Oulx: 1100 m: 1-15 VIII 1925: Verity [leg.].

*macroproto (nn)—*Sloperia proto macroproto* Verity, 1928—Bull. Soc. ent. Fr. 1928:141—Replacement name for *Muschampia proto gigas* Verity, 1925, said to be preoccupied by *Pyrgus gigas* Bremer, 1864. There is neither primary nor secondary homonymy (at present and at the time of the replacement) between the two names.

macta (nn)—*Adopoea flava macta* Verity, 1926—Entomologist's Rec. J. Var. 38:104—Replacement name for an unavailable infrasubspecific name *Adopoea flava major* Tutt, 1906, said to be preoccupied by *Adopoea lineola major* Tutt, 1906—Treated as (and probably raised to) a subspecies by Kauffmann (1951): *Thymelicus silvestris mactus* [nec Verity].

MAGNAGALLICA (nn)—*Hesperia serratulae magnagallica* Verity, 1931—Bull. Soc. ent. Fr. 1931:201—Replacement name for *Hesperia serratulae occidentalis* Lucas,1910, said to be preoccupied by *Pyrgus occidentalis* Skinner, 1906 (i.e. secondary homonymy); according to Jong (1972) *Pyrgus serratulae serratulae magnagallicus* is only an infrasubspecific form, i.e. a taxon subjectively not worthy of recognition.

*magnalveus (ra)—*Hesperia alveus magnalveus* Verity, 1929—Mus. barcin. Scienc. nat. Op. 11(4):12—Syntypes 5♂♂, 1♀ [N. Italy: Piemonte]: Alpi Cozie: Val Susa: Oulx: 1100 m: 6 VII-11 VIII 1925: Verity [leg.].

magnatages (sf, ra)—*Erynnis tages magnatages* Verity, 1938—Entomologist's Rec. J. Var. 50:(1)—Syntypes 11♂♂ [N. Greece]: Macedonia: Olympus: [Skala]: 300 m: 20 VI-25 VII 1936—Romei [leg.].

magnaustralis (sf)—*Erynnis alceae magnaustralis* Verity, 1924—Entomologist's Rec. J. Var. 36:106—Syntypes 2♂♂ Italia centr[ale]: Toscana]: Lucca: Valle Camaione: 300 m: 10-18 VII 1923: Querci [leg.]—Warren (1926): synonym of *Erynnis alceae australis* Zeller, 1847.

majornitida (sr)—*Adopoea lineola major majornitida* Verity, 1940—Syntypes 2♂♂ [N. Italy]: Torino: Venaria: 24 VI & 2 VII 1903: Rocci [leg.].

*maxima (ra)—*Adopoea flava maxima* Verity, 1936—Entomologist's Rec. J. Var. 48:(3)—Syntypes 9♂♂, 8♀♀ [N. Greece]: Macedonia: Salonika (= Thesaloniki): [ca. 300 m]: 3-7 VI 1935: Romei [leg.].

medioalbodetersa (if)—*Spialia hibiscae medioalbodetersa* Verity, 1940—Le farfalle diurne d'Italia 1:77—Italy: Toscana: Appennino Pistoiese: Abetone: 1400 m.

megalegyna (if)—*Gegenes nostrodamus nostrodamus megalegyna* Verity, 1940—Le farfalle diurne d'Italia 1:125—Holotype ♂ [Italy: Sicily]: Palermo: M. Maggiore: 22 VI [1]920.

melotiformis (if)—*Hesperia malvoides melotiformis* Verity, 1929—Mus. barcin. Scient. nat. Op. 11(4):7—Holotype ♂ Italia centrale: Toscana: Firenze: Pian di Mugnone: 200 m: 8 VIII 1917: Querci [leg.]—Holotype by implication: described from a single specimen.

microcarthami (nn)—*Hesperia carthami microcarthami* Verity, 1928—Bull. Soc. ent. Fr. 1928:140—Replacement name of an unavailable infrasubspecific name *Hesperia carthami pyrenaica* Warren, 1926, proposed originally for an infrasubspecific race, said to be preoccupied by an apparently available name *Hesperia malvae pyrenaica* Tutt, 1906, originally propsed for a var[iety] to be interpreted as of subspecies-rank (i.e. available name). Jong (1972) erroneously interpreted Warren's name as available for a subspecies.

minuta (sf)—*Augiades sylvanus sylvanus minuta* Verity, 1920—Boll. Lab. Zool. gen. agr. R. Scuola Agric. Portici 14:44—Syntypes 3♂♂, 1♀ Italia centrale: [Toscana]: Lucca: Fiume Camaione: 300 m: 6-7 IX 1915: Querci [leg.].

*modestior (ra)—*Hesperia malvoides modestior* Verity, 1929—Mus. barcin. Scient. nat. Op. 11(4):7—Syntypes 5♂♂ Italia centrale: Toscana: Firenze: Pian di Mugnone: 200 m: 21 VII 1915, 7-8 VIII 1917, 12 IX 1915—Jong (1972): *Pyrgus malvoides modestior* (ssp.).

*necaccreta (ra)—*Hesperia alveus necaccreta* Verity, 1929—Mus. barcin. Scient. Op. 11(4):12—Syntypes 6♂♂, 5♀♀ [Spain]: Catalogne: Nuria: 28 VII [19]25; 1♂ [France]: Pyr[enees]-Or[ientales]: Porte: 20 VII [19]25; (all) ex coll. Stempffer—Jong (1972): synonym of *Pyrgus alveus accretus* Verity, 1925.

*nigrita (ra)—*Muschampia proto nigrita* Verity, 1925—Entomologist's Rec. J. Var. 37:54—Syntypes 5♂♂, 2♀♀ Espana: Nueva Castilla: [Cuenca: 1200 m]—Warren (1926): *Sloperia proto nigrita* (infrasubspecific race).

*nigrobscurata (ra)—*Carcharodus lavatherae nigrobscurata* Verity, 1938—Entomologist's Rec. J. Var. 50:(1)—Syntypes 1♂, 1♀ [N. Greece]: Macedonia: Olympus:

[Skala]: 300 m: 23 VI & 8 VII 1936: Romei [leg.].

nigrocarens (if)—*Hesperia fritillum nigrocarens* Verity, 1925—Entomologist's Rec. J. Var. 37:72—Name for a specimen illustrated by Reverdin (1910) in Bull. Soc. lepid. Geneve 2: pl. 4, fig. 11 from Switzerland: Jura Bernois: Tramelan—Warren (1926): synonym of *Hesperia fritillum* Denis & Schiffermüller, 1775.

*****nigropicta** (ra)—*Hesperia bellieri nigropicta* Verity, 1926—Entomologist's Rec. J. Var. 38:103—Syntypes 9♂♂, 5♀♀ [N. Italy: Piemonte]: Alpi Cozie: Val Susa: Oulx: 1100 m: 16 VII-11 VIII 1924: Verity [leg.]—Jong (1972): infrasubspecific form of *Pyrgus bellieri bellieri* Oberthür, 1910.

nigrosatura (sr)—*Hesperia onopordi nigrosatura* Verity, 1925—Entomologist's Rec. J. Var. 37:73—Syntypes 5♂♂ Morocco: Fez: VIII 1921: [Lucas leg.]—Warren (1926) treated the taxon as an aberration.

*****oberthueri** (ra)—*Erynnis boetica oberthueri* Verity, 1919—Entomologist's Rec. J. Var. 31:27—Name for specimens illustrated by Oberthür (1911) in Etud. Lepid. comp. 5: fig. 605, 606 from S. Italy: Sicily—Warren (1926): infrasubspecific race of *Spilothyrus baeticus octodurensis* Oberthür, 1911.

obscurata (if)—*Erynnis stauderi obscurata* Verity, 1925—Entomologist's Rec. J. Var. 37:44—Algeria.

*****occidentalis** (ra)—*Hesperia sidae occidentalis* Verity, 1919—Entomologist's Rec. J. Var. 31:27—Syntypes 10♂♂, 3♀♀ Italia centrale: Toscana: Firenze: Fiesole: Pian di Mugnone: 200 m; M. Fanna: 650 m: 27-29 V 1915, 9-29 V 1916, 27-31 V 1917, 17 V-10 VI 1917: Querci [leg.]—Warren (1926): *Hesperia sidae occidentalis* (ssp.).

OCCIDUA (nn)—*Hesperia sidae occidua* Verity, 1925—Entomologist's Rec. J. Var. 37:76—Replacement name for *Hesperia sidae occidentalis* Verity, 1919, said to be preoccupied by *Hesperia serratulae occidentalis* Lucas, 1910—Evans (1949): *Pyrgus sidae occidua* (ssp.); Jong (1972): *Pyrgus sidae occiduus* (ssp.).

onopordiformis (if)—*Hesperia armoricanus onopordiformis* Verity, 1919—Entomologist's Rec. J. Var. 31:27—Name for specimens illustrated by Oberthür (1910) in Etud. Lepid. comp. 4: pl. LVII, figs. 509, 510 from Italy: Toscana; original rank confused, probably individual form or aberration.

onopordimima (if)—*Pyrgus serratulae fritillum onopordimima* Verity, 1940—Le farfalle diurne d'Italia 1:57—Holotype ♂ [N. Italy]: Alpi Maritime: Terme di Valdieri: 3-16 VIII [19]38: Verity [leg.]; *onopordimina*.

*****orae** (ra)—*Urbicola comma orae* Verity, 1924—Entomologist's Rec. J. Var. 36:107—Syntypes 3♂♂, 2♀♀ [C. Italy: Toscana]: Livorno: Quercianella: 5-22 VIII [19]22; Spezia: Pertusola: 21 VIII [19]13: [Verity leg.].

pallidissima (sf, ra)—*Hesperia onopordi pallidissima* Verity, 1925—Entomologist's Rec. J. Var. 37:73—Spain: Prov. Teruel: Sierra de Albarracin—Treated as aberration by Warren (1926).

pallidissimefulva (sf)—*Hesperia onopordi pallidissimefulva* Verity, 1925—Entomologist's Rec. J. Var. 37:74—Spain: Prov. Teruel: Sierra de Albarracin—Treated as a synonym of *Hesperia onopordi fulvotincta* Verity, 1919, by Warren (1926).

parafabressei (if)—*Hesperia fritillum parafabressei* Verity, 1925—Entomologist's Rec. J. Var. 37:72—Name for a specimen from S. France: Digne, illustrated by Oberthür (1912) in Etud. Lepid. comp. 6: pl. CXLI, fig. 1280—Warren (1926): synonym of *Hesperia fritillum iberica* Grum-Grshimailo, 1893; Jong (1972): infrasubspecific form of *Pyrgus cirsii* Rambur, 1842.

parvula (sf)—*Powellia sao sao parvula* Verity, 1921—Entomologist's Rec. J. Var. 33:173—Syntypes 1♂, 1♀ Italia settentrionale: Alto Adige: Tirolo: Atzwang: 30 VII [19]20—Warren (1926): *Powellia sertorius gracilis parvula* (aberration); Jong (1974): *Spialia sertorius sertorius parvula* (seasonal form).

*****picena** (ra)—*Hesperia foulquieri picena* Verity, 1920—Entomologist's Rec. J. Var. 32:4—Syntypes 4♂♂, 1♀ Italia centrale: Macerata: Piceno: Monti Sibillini: Bolognola: 1200 m: 4 IX 1913, 18 VIII 1918, 2 IX 1919: Querci [leg.]—Warren (1926): *Hesperia foulquieri bellieri picena* (infrasubspecific race); Evans (1949): *Pyrgus bellieri picena* (ssp.); Jong (1972): *Pyrgus bellieri picenus* (ssp.).

*****planorum** (ra)—*Hesperia serratulae planorum* Verity, 1925—Entomologist's Rec. J. Var. 37:56—Syntypes 1♂, 1♀ [Germany]: Friedland i[n] M[ecklenburg]—Warren (1926): *Hesperia serratulae planorum* (infrasubspecific race); Jong (1972): synonym (by implication) of *Pyrgus serratulae serratulae* Rambur, 1829 (as infrasubspecific form).

postaltheae (sf)—*Spilothyrus altheae postaltheae* Verity, 1934—Entomologist's Rec. J. Var. 46:(5)—Syntypes 2♂♂, 1♀ [N. Italy]: Alpi Cozie: Val Susa: Oulx: 1100 m: 7-10 VIII 1925: Verity [leg.].

postgenita (sf)—*Hesperia onopordi conyzae postgenita* Verity, 1926—Entomologist's Rec. J. Var. 38:104—Syntypes 19♂♂, 3♀♀ [N. Italy: Piemonte]: Alpi Cozie: Val Susa: Oulx: 1100 m: 2-12 VIII 1925: Verity [leg.]—Warren (1926): synonym of infrasubspecific race *Hesperia onopordi fulvotincta* Verity, 1926.

postorientalis (sf)—*Spilothrus orientalis postorientalis* Verity, 1928—Bull. Soc. ent. Fr. 1928:140—Turkey: Constantinople.

postpersica (sf)—*Pyrgus armoricanus postpersica* Verity, 1936—Entomologist's Rec. J. Var. 48:(3)—Greece: Macedonia: Olympus: up to 1000 m: VIII-IX.

postquercii (sf)—*Pyrgus onopordi quercii postquercii* Verity, 1940—Le farfalle diurne d'Italia 1:50—Italy: Modena: Scandianese: Borzano: Tana Musina: 16 VII.

posttesselloides (nomen nudum)—*Spialia orbifer posttesselloides* Verity, 1938—Entomologist's Rec. J. Var. 50:(4)—Name proposed for seasonal form of second generation published in the heading of paragraph without description, definition or indication, confused probably by reference to *tesselloides* Herrich-Schaffer, 1845. The same author (Verity, 1940) perhaps "validated" the name for seasonal form of second generation from Greece: Olympus: Skala: 350 m. Jong (1974) treated *Spialia orbifer orbifer posttesselloides* as seasonal form of second generation; Evans (1949) synonymized *posttesselloides* with *Spialia sertorius* Hoffmansegg, 1804. It is interesting to compare the views of two acknowledged authorities on the identity of a hitherto undescribed taxon.

posttutti (sf)—*Pyrgus malvae malvoides tutti posttutti* Verity, 1940—Le farfalle diurne d'Italia 1:41—Italy: Milano: Doria; Alto Adige: Ponte all'Isarco.

praeaustralis (sf)—*Erynnis alceae australis praeaustralis* Verity, 1924—Entomologist's Rec. J. Var. 36:106—Syntypes 3♂♂ [S. Italy]: Isola di Sicilia: Palermo: Monreale: San Martino: 800 m: 25-29 V 1919: Querci [leg.]—Warren (1926): synonym of *Erynnis alceae australis* Zeller, 1847.

pseudomalvae (nomen nudum)—*Hesperia malvae malvoides pseudomalvae* Verity, 1913—Boll. Soc. ent. ital. 44(1912):208—Name proposed for race published without description, definition or indication, later "validated" for seasonal form.—Warren (1926): synonym of *Hesperia malvoides* Elwes & Edwards, 1898.

pseudomalvae (sf)—*Pyrgus malvae malvoides modestior pseudomalvae* Verity, 1940—Le farfalle diurne d'Italia 1:42—Syntypes 1♂, 3♀♀ [C. Italy: Toscana]: Firenze: Pian di Mugnone: 20 V[19]35, 2 VI [19]29, 2 V [19]29: Verity [leg.].

*__pulchracteon__ (ra)—*Thymelicus acteon pulchracteon* Verity, 1940—Le farfalle diurne d'Italia 1:104—Syntypes 6♂♂, 2♀♀ [C. Italy]: Abruzzi: Gran Sasso: 1700 m: 2 VIII 1939: Romei [leg.].

*__pumilionimima__ (ra)—*Gegenes nostrodamus pumilionimima* Verity, 1940—Bull. Soc. ent. ital. 63:111—Syntypes 9♂♂ [Italy]: Costa Toscana: Viareggio: Pineta Arciducale: 31 VIII-14 IX [19]27: Verity [leg.].

*__pyreneialpium__ (ra)—*Hesperia alveus pyreneialpium* Verity, 1929—Mus. barcin. Scient. nat. Op. 11(4):11—Syntypes 9♂♂ [S. France: Hautes-Pyrenees]: Gedre: VII [19]15, 15-19 VII 1926: Rondou [legh.]—Some specimens with incomplete data and/or damaged by museum pests.

*__ragusai__ (ra)—*Thymelicus acteon ragusai* Verity, 1919—Entomologist's Rec. J. Var. 31:28—Syntypes 5♂♂, 1♀ [S. Italy]: Sicilia: Ragusa [leg.]; Isola di Sicilia: Palermo: Monreale: San Martino: 3 & 10 VI 1918: Querci [leg.].

retrograda (if)—*Spialia hibiscae therapne retrograda* Verity, 1940—Le farfalle diurne d'Italia 1:80—Holotype ♂ [France]: Corse: Evira: 20 VI [19]24; *retrograda*.

*__rostagnoi__ (ra)—*Erynnis boetica rostagnoi* Verity, 1919—Entomologist's Rec. J. Var. 31:27—Holotype ♂ Italy: Lazio: Oricola: [900 m]: 4 VIII [19]13: Rostagno [leg.]; described from a single specimen—Warren (1926): aberration of *Spilothyrus baeticus* Rambur, 1839.

rubescens (sf)—*Hesperia onopordi rubescens* Verity, 125—Entomologist's Rec. J. Var. 37:74—Name proposed conditionally for seasonal form of third generation hitherto not previously recorded but expected in S. France—Warren (1926): synonym of infrasubspecific race *Hesperia onopordi fulvotincta* Verity, 1919, which was proposed originally as seasonal form of second generation.

rufosatura (sf)—*Hesperia armoricanus rufosatura* Verity, 1925—Entomologist's Rec. J. Var. 37:73—Syntype 1♀ Italy: Toscana: Firenze: Fontebuona di Vaglia: 350 m: 24 VIII [????]: [Querci leg.]; original designation confused, probably seasonal form—Warren (1926): synonym of *Hesperia armoricanus fulvoinspersa* Verity, 1919, treated as infrasubspecific race; Jong (1972): synonym of seasonal form *Pyrgus armoricanus armoricanus corsiens* Oberthür, 1919.

*__septentrionalis__ (ra)—*Augiades sylvanus septentrionalis* Verity, 11919—Entomologist's Rec. J. Var. 31:28—Syntypes 2♂♂, 4♀♀ Inghilterra (= England).

***siccior** (ra)—*Spilothyrus altheae siccior* Verity, 1934—Entomologist's Rec. J. Var. 46:(5)—Syntypes 7♂♂ [N. Italy: Alpi Marittime: Terme di] Valdieri: [1400 m]: 23 VII [19]09, 13-20 VII [19]11: [Verity leg.].

***speciosa** (ra)—*Hesperia carthami speciosa* Verity, 1921—Entomologist's Rec. J. Var. 33:172—Syntypes 11♂, 1♀ [N. Italy]: Sudtirol: [Isarco Valley (= Eisacktal)]: 191[?]: Wagner [leg.]; data incomplete, partly by implication—Warren (1926): synonym of ssp. *Hesperia carthámi valesiaca* Mabille, 1875.

subclarus (sf, ra)—*Nisoniades tages subclarus* Verity, 1921—Entomologist's Rec. J. Var. 33:172—Syntypes 1♂, 1♀ Italia settentrionale: Alto Adige: Atzwang: 30 VII [19]20: [Verity leg.].

subconyzae (sf)—*Hesperia onopordi subconyzae* Verity, 1925—Entomologist's Rec. J. Var. 37:74—Italy: Toscana: Firenze.

subgracilis (sf)—*Powellia sao gracilis subgracilis* Verity, 1921—Entomologist's Rec. J. Var. 33:173—Syntypes 23♂♂, 5♀♀ C. Italy: Toscana: Firenze; all ex glass case, remounted and relabelled, six specimens from the original type-series of 34 destroyed after heavy damage by museum pests—Jong (1974): seasonal form *Spialia sertotius sertorius subgracilis*.

***superalpina** (ra)—*Urbicola comma superalpina* Verity, 1928—Bull. Soc. ent. Fr. 1928:127—Syntypes 6♂♂, 3♀♀ [N. Italy]: Alpi Retiche: Bormio: 1300 m: 1-13 VIII [19]27: Verity [leg.].

suprabellieri (if)—*Hesperia foulquieri suprabellieri* Verity, 1920—Entomologist's Rec. J. Var. 32:4—Holotype ♂ It[alia] cent[rale]: Macerata: Monti Sibillini: Bolognola: 1200 m: 22 VIII 1919: Querci [leg.]; type: *suprabellieri*—Warren (1926): *Heseria foulquieri picena suprabellieri* (aberration).

tersa (sf)—*Hesperia armoricanus tersa* Verity, 1924—Entomologist's Rec. J. Var. 36:107—Syntypes 1♂, 1♀ Italia centr[ale: Toscana]: Lucca: Valle Camaione: 300 m: 2-3 & 10-18 VII 1923: Querci [leg.]—Warren (1926): synonym of infrasubspecific race *Hesperia armoricanus fulvoinspersa* Verity, 1919.

tersior (sf)—*Hesperia onopordi tersior* Verity, 1924—Entomologist's Rec. J. Var. 36:107—Syntype(?) 1♂ Italia centrale: [Toscana]: Lucca: Valle Camaione: 10-16 VIII 1923: Querci [leg.]; status of specimen uncertain—Warren (1926): synonym of infrasubspecific race *Hesperia onopordi fulvotincta* Verity, 1919.

tersissima (sf)—*Hesperia onopordi tersissima* Verity, 1925—Entomologist's Rec. J Var. 37:74—C. Italy: Toscana: Firenze—Warren (1926): synonym of infrasubspecific race *Hesperia onopordi fulvotincta* Verity, 1919.

THRACIMIMA (sp)—*Hidari thracimima* Verity, 1931—Bull. Soc. ent. Fr. 1931: 199—Holotype ♂ [S.] China: Canton: [ex O. Bang-Haas]; tipo: *thracimima*—Described from a single specimen—Evans (1949): junior subjective synonym of *Hidari irava* Moore, 1857.

***tripolina** (ra)—*Erynnis alceae tripolina* Verity, 1925—Entomologist's Rec. J. Var. 37:54—Syntypes 6♂♂, 2♀♀ Nord-Africa: Tripolitania: Garian [plateau]: 700 m: 1-7 V 1924: Romei [leg.]—Warren (1926): infrasubspecific race of *Erynnis alceae australis* Zeller, 1847; Evans (1949): *Carcharodus alceae tripolina* (ssp.).

***tutti** (ra)—*Hesperia malvoides tutti* Verity, 1919—Entomologist's Rec. J. Var.

31:28—Name for specimen from Switzerland: Locarno described by Tutt (1906) in British Butterflies 1:225—Warren (1926): aberration of *Hesperia malvoides* Elwes & Edwards, 1898.

venusta (sf)—*Hesperia onopordi venusta* Verity, 1925—Entomologist's Rec. J. Var. 37:73—Name for specimen illustrated by Oberthür (1910) in Etud. Lepid. comp. 4: pl. LVII, fig. 527—Warren (1926): synonym of *Hesperia onopordi* Rambur, 1842.

viridescens (if)—*Erynnis marrubii fulvescens viridescens* Verity, 1925—Entomologist's Rec. J. Var. 37:43—France: Marseille(?)—Warren (1926): aberration of *Spilohyrus baeticus* Rambur, 1839—Treated as (and probably raised to) subspecies by Manley & Allcard (1970): *Carcharodus boeticus viridescens* [nec Verity].

*warrenensis (ra)—*Hesperia alveus warrenensis* Verity, 1928—Bull. Soc. ent. Fr. 1928:140—Name for specimens figured by Warren (1926) in Trans. ent. Soc. Lond. 74:120, pl. 43—Jong (1972): *Pyrgus warrenensis* (sp.).

Postscript. Mr. Paddy McHenry was kind enough to draw to the attention of the senior author the inexcusable omission of four North American infrasubspecific names proposed by R. Verity and not listed in the catalogue (Kudrna, 1983) of his names. Mr. McHenry's critical notes made in his letter of 15 VIII 1983 are gratefully acknowledged. The missing names are listed below in alphabetic order (Kudrna, 1983); family name is given in square brackets at end of each entry.

cocandicides (ra)—*Colias nastes rossi cocandicides* Verity, 1911—010:355—N. Canada: Barren Grounds—[Pieridae].

mira (ab)—*Colias pelidne mira* Verity, 1911—010:347—Labrador—[Pieridae].

minor (fm)—*Parnassius delius smintheus smintheus minor* Verity, 1911—010:xx—British Columbia—Name proposed without description or definition for a specimen figured on pl. XVI, fig. 21—[Papilionidae].

pseudocorybas (ra, fm)—*Parnassius delius delius pseudocorybas* Verity, 1907—010:107—U.S.A.: Montana—Original combination and rank confused but certainly infrasubspecific name—[Papilionidae].

Additonally, an unfortunate error was overlooked in the table showing the dates of publication of Verity's "Rhopalocera palearctica" (cf. Kudrna, 1983:10): 2nd installment which was published 30 XI 1905 was accompanied also by plate V (i.e. plates V-VII). Furthermore, it appears that the true date of publication of Verity's paper listed as item **55** (cf. Kudrna, 1983:13-14) could differ from the date stated by the publishers of the journal concerned. The paper was certainly published not later than 1927, but somewhat earlier publication cannot be ruled out. The revised bibliographical reference should read: Arch. Naturgesch. (A)91(9):102-120. The above errors are regretable but perhaps not entirely unexpected owing to both the complexity and sheer amount of work involved. Should any further similar errors come to light, a note pointing them out by the readers concerned would be appreciated.

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Revision of the Oriental and Nearctic Genus *Ellabella* (Lepidoptera: Copromorphidae)

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Abstract. The genus *Ellabella* Busck is revised, and two new species (*E. bayensis*, n. sp., and *E. johnstoni*, n. sp.) are added to the two described western Nearctic species (*E. editha* Busck and *E. melanoclista* (Meyrick)) and the single known Chinese species (*E. chalazombra* (Meyrick)). The genus is transferred to Copromorphidae. The host of one *Ellabella* species, *Mahonia* (Berberidaceae) (De Benedictis, 1984), and the distributions of *Ellabella* and *Mahonia* indicate that *Mahonia* or other Berberidaceae may be the hosts of the other species, including the Chinese *Ellabella*.

Introduction

The genus *Ellabella* has had an interesting history since its original description (Busck, 1925) and since the description of its two generic synonyms, *Probolacma* Meyrick (1927) and *Spilogenes* Meyrick (1938). Whereas *Ellabella* was originally described in the family Glyphipterigidae, the other two genera were described as Yponomeutidae (Heppner, 1982). Clarke ([1965]) later synonymized *Probolacma* with *Ellabella*, placing the genus in Ethmiidae, while leaving *Spilogenes* in Yponomeutidae. *Ellabella* was removed from Ethmiidae by Powell (1973). My initial studies of the genus prompted a transfer of *Ellabella* to Plutellidae (Heppner, 1978), yet *Ellabella* has remained an enigmatic group.

It was originally my belief, as that of Busck (1925), that *Ellabella* had some relationship with *Lotisma* Walsingham. Furthermore, I viewed both genera as belonging to the family Copromorphidae, a family not previously known to occur in the Nearctic region. *Ellabella* was placed in Plutellidae (Heppner, 1978), however, primarily because of a similarity in adult characters between *Ellabella* and another unusual genus, *Araeolepia* Walsingham. It is yet unclear if *Araeolepia* should remain in Plutellidae, but the newly discovered larval characters of *Ellabella* (DeBenedictis, 1984) support the view that *Ellabella* should be considered a copromorphid. One of the main reasons for this uncertainty is a lack of information. We do not yet know the immature stages of *Araeolepia* and, until recently, this was likewise the case for *Ellabella*. Another difficulty involves the lack of clear distinguishing family characters between Copromorphidae and Plutellidae that are consistent for the adults. Typical copromorphids have

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[1] Contribution No. 582, Bureau of Entomology, FDACS, Division of Plant Industry.

long radial and median veins in the forewings, maxillary palpi with only 1-2 segments, more porrect labial palpi than Plutellidae, and usually distinct scale tufts on the forewings, among other characters. Typical Plutellidae show largely the opposite character, notably 4-segmented maxillary palpi and rather upcurved labial palpi but with large medial scale tufts ventrally that simulate porrect palpi. *Ellabella* presents somewhat of a middle ground on adult characters, other than the unusual genitalia. Inasmuch as most plutellid larvae have a prothoracic L-group that is trisetose, and *Ellabella* larvae are bisetose (DeBenedictis, 1984), as are most other Copromorphidae larvae, it now appears more likely that the genus is a copromorphid.

The Plutellidae are too little studied on a world basis. The family limits of the Plutellidae have not yet been defined clearly enough and, thus, genera remain in Plutellidae that have characters atypical for the family: for example, the Galacticinae have 2-segmented maxillary palpi and bisetose larvae, as do a few other odd plutellid genera that conform to adult plutellid characters in general. The Yponomeutidae also require redefinition. A thorough generic study of world genera of Copromorphidae and Plutellidae, as well as Yponomeutidae, is needed in order to associate all the genera with these families and to redefine family limits.

In the present paper the Chinese species, *Ellabella chalazombra* (Meyrick), is redescribed and two new Nearctic species are described for a total of four Nearctic species. No other *Ellabella* are known thus far nor are any species known other than in east Asia or the New World, although it is probable that one or more of the United States species will also be found in northern Mexico. The disjunct distribution of *Ellabella*, as the genus is now delimited, does not appear so unusual in the light of the recent discovery of the host plant of the new California species by J. DeBenedictis (1984), since the host genus is also found in China. Such disjunct distributions between western North America and eastern Asia, are found in other western moths and among many plant groups. Among moths another example is the tribe Hilarographini of Tortricidae, in which North American species are very closely related to some species from Japan (Heppner, 1983). Among plants there are a number of so-called Tertiary relicts in western North America with affinities or nearest relatives in east Asia. Some American endemics are well-known examples: the redwoods, *Sequoia* and *Sequoiadendron* (Taxodiaceae), from California, have their nearest relative (*Metasequoia*) in China (Raven, 1977). This is likewise true for the host plant group of at least one *Ellabella*, in Berberidaceae: the single verified host is *Mahonia pinnata* (Lag.) Fedde. The plant genus *Mahonia* (some botanists consider this only a subgenus of *Berberis*) is distributed over much of montane North America at elevations of about 1300-3000 meters, although sometimes at lower elevations in areas such as coastal California. Figure 1 shows montane areas of North America at
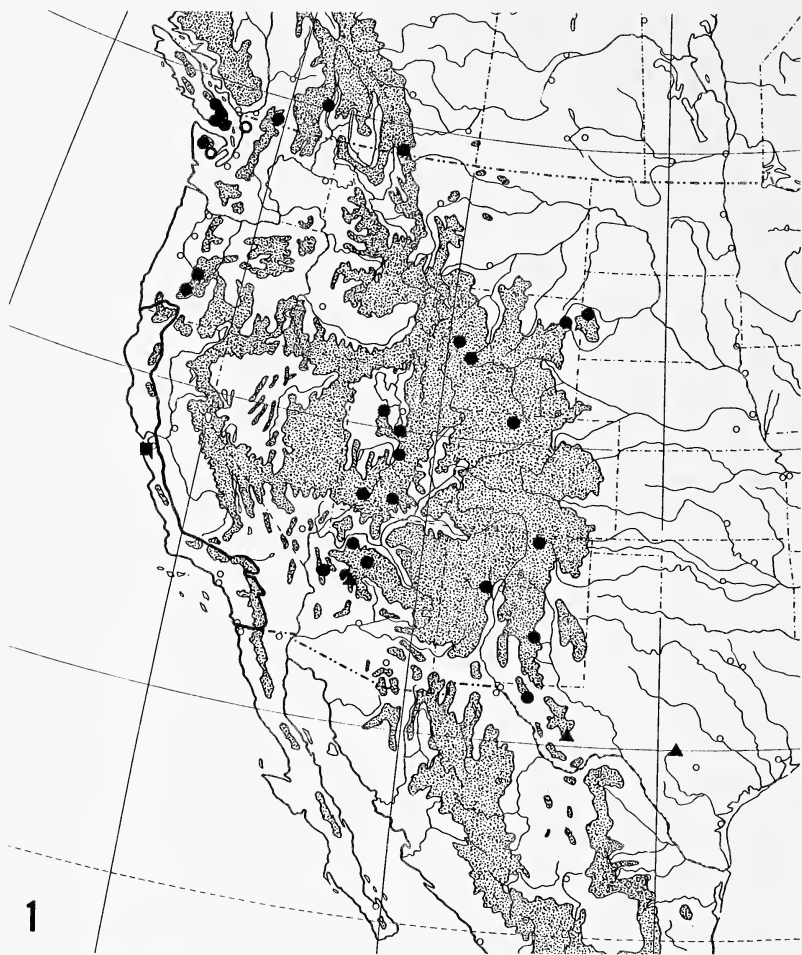
Fig. 1. Distribution map of *Ellabella* species in North America: *E. bayensis*, n.
sp. (■); *E. editha* Busck (●); *E. johnstoni*, n. sp. (○); *E. melanoclista*
(Meyrick) (▲). Shaded areas correspond to the 1500 meter elevation
and also the approximate range of *Mahonia* plants. The demarcation
line in California indicates the limit of distribution of *Mahonia pinnata*,
the host of *Ellabella bayensis*.

approximately the 1500 meter contour line. This area (north of Mexico)
corresponds fairly well to the distribution of North American *Mahonia*
(Ahrendt, 1961). The known localities of *Ellabella* species in North
America also correspond to this delimited area of montane habitats.

There are 50 known species of *Mahonia* in North America and east Asia.
The distribution of *M. pinnata*, however, is limited to California and

southern Oregon (as indicated by the heavy line in Figure 1). Thus far the new species of *Ellabella* utilizing this host has not been collected outside of this distribution range. Likewise, a population of *Ellabella editha* (Busck), from Waterton Lakes, Alberta, indicates that a possible host is *Mahonia repens* (Lindl.) G. Don, since this is the only known species of *Mahonia* found in Alberta, and its overall distribution from Alberta and British Columbia to central Texas and Arizona coincides with the total distribution of *Ellabella editha*. One can only speculate that all *Ellabella* may be restricted to *Mahonia* species, since we do not yet know if the moths are restricted to only one species of *Mahonia*, or indeed even only to this single plant genus.

The *Mahonia* species of east Asia (Ahrendt, 1961) occur most frequently in the broadleaf evergreen forests of China and adjacent areas (after Wang, 1961), as shown in the shaded area of Figure 2. Figure 2 shows a plant association area and should not be confused with Figure 1, where an altitudinal limit is shown. The shaded area in Figure 2 also envelopes the single locality known for *Ellabella chalazombra*. Assuming the Chinese *Ellabella* utilizes a *Mahonia* as a larval host, then the moth species may be distributed more widely within the forest zone shown on the map. *Mahonia* does not occur naturally in Japan (it has been introduced as an
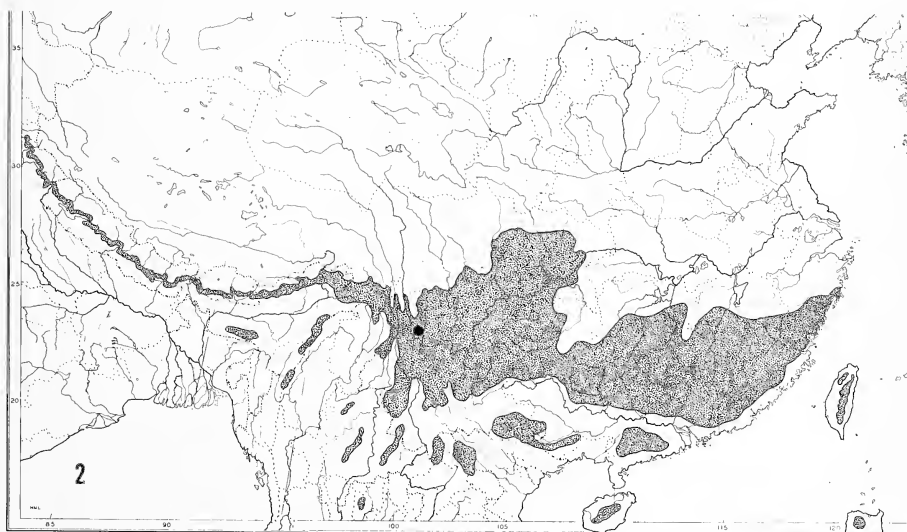

Fig. 2. Distribution map of *Ellabella chalazombra* (Meyrick) (Likiang, Yunnan, China) and the known limits of Oriental broadleaf evergreen forest (oaks, schima, laurels) [outside of Japan] where *Mahonia* species are concentrated (after Wang, 1961). Outlying areas with *Mahonia* species in southern Asia include southern India (Nilgiri Hills), northern Sumatra, and the Philippines (Luzon).

ornamental), and inasmuch as Japanese collectors have very diligently surveyed Japan for moths, it appears that *Ellabella* does not occur in Japan. According to Ahrendt (1961), *Mahonia* has disjunct species in southern India (Nilgiri Hills), northern Sumatra, and the Philippines (Luzon), but no *Ellabella* have been found in these regions.
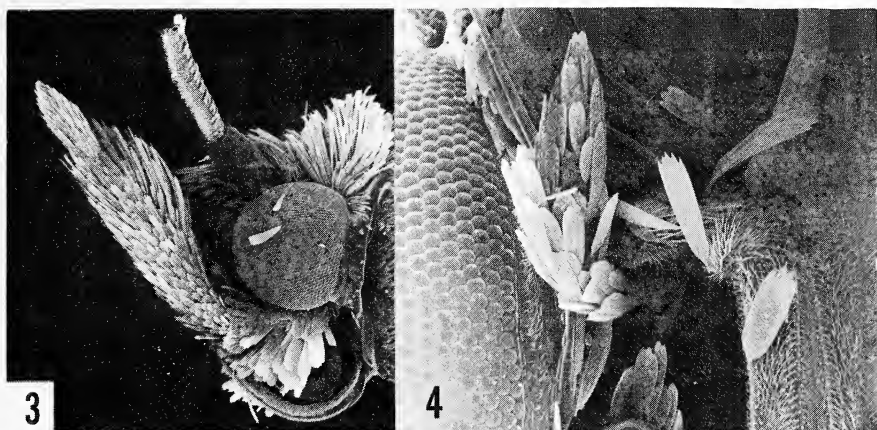
Ellabella Busck

Ellabella Busck, 1925:46 (Type-species.-*Ellabella editha* Busck, 1925: 48, by original designation).

Probbolacma Meyrick, 1927:362 (Type-species.-*Probolacma melanoclista* Meyrick, 1927:362, by monotypy).

Spilogenes Meyrick, 1938:19 (Type-species.-*Spilogenes chalazombra* Meyrick, 1938:19, by monotypy).

Adult. Small moths, 8-13 mm forewing lengths. **Head** (Figure 3, 5): vertex with somewhat roughened scale tufts; frons smooth scaled; labial palpus straight, somewhat upwards tilt (often held in porrect position), with long median segment (usually ca. 3X length of short apical segment); maxillary palpus (Figures 4, 6) prominent, 4-segmented; haustellum large, unscaled; pilifer large; compound eye large; ocellus very small (in relation to compound eye); antenna (Figures 3, 5) filiform with short ventral setae, length of antenna about ½ forewing length, little sexually dimorphic; antennal scape lacking pecten. **Thorax:** normal but with large dorsal median scale tuft; legs with 0-2-4 tarsal formula. **Forewing** (Figure 7): elongate with pointed apex, oblique termen and rounded tornus; all veins present and separate; R^5 to termen near apex; chorda vestigial; M_1 convergent with M_2 at base; CuA_1 and CuA_2 curved and parallel; CuP present near tornus; A_1+_2 with short basal fork; A_3 very small. **Hindwing** (Figure 7): elongate, subovate, with blunt pointed apex and slightly oblique termen; all veins present; R_5 separate from Sc; median veins equidistant; M_3 convergent with CuA_1 at base (more separate in *E. chalazombra*); CuA_1 and CuA_2 relatively straight and parallel; CuP long, from termen; A_1+^2 curved, with small basal fork; A_3 long; A_4 minute. **Abdomen:** normal but males with two pairs of large ventral coremata, one pair on sternite 2 (Fig. 8) and one pair between sternites 7 and 8, the latter pair in internal pouches (Fig. 9); posterior coremata have exterior sclerotized borders along anterior margin of pouch openings, shaped as two half circles meeting at a median notch. **Male genitalia:** uncus and gnathos well developed; gnathos with two strong lateral arms joined distally as spined ends; socius absent; transtilla strong but tending to be incompletely fused medially; valva relatively simple, setaceous and elongate, with small carinate ridges or relatively smooth; anellus a V- or U-shaped plate with variously shaped appendages and median spined juxta; tegumen normal; vinculum reduced, quadrate; saccus undeveloped; aedeagus elongate, with phallobase and single cornutus. **Female genitalia:** ovipositor of average length (not noticeable elongated or shortened for the total genitalia size); setaceous papilla analis; apophyses stout, anterior pair shorter than posterior pair and usually stronger; posterior genital plate with varying degree of projecting central point (flat on sternite); ostium a simple membranous funnel leading to a membranous ductus bursae having a sclerotized collar near the entrance of the ductus seminalis; corpus bursae simple, ovate; signum a rugose plate with short

Figs. 3-4. Head morphology of *Ellabella editha* Busck: 3, profile; 4, detail of
haustellum base, maxillary palpus, and pilifer (USNM slide 77334,
South Dakota).
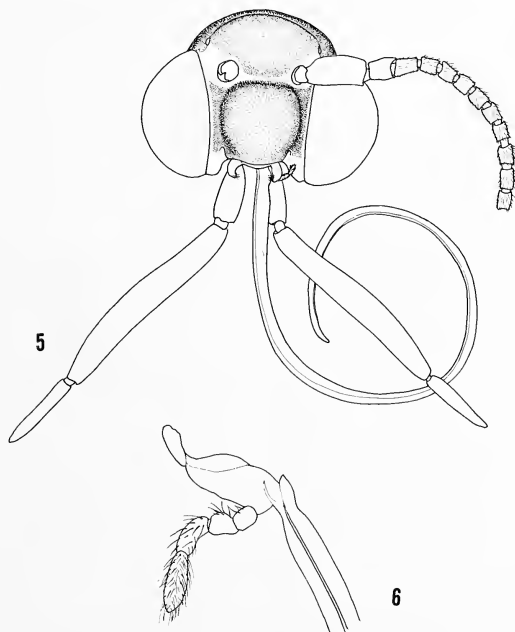
Figs. 5-6. Head morphology of *Ellabella editha* Busck: 5, head frontal view; 6,
detail of maxillary palpus and haustellum (USNM slide 77710,
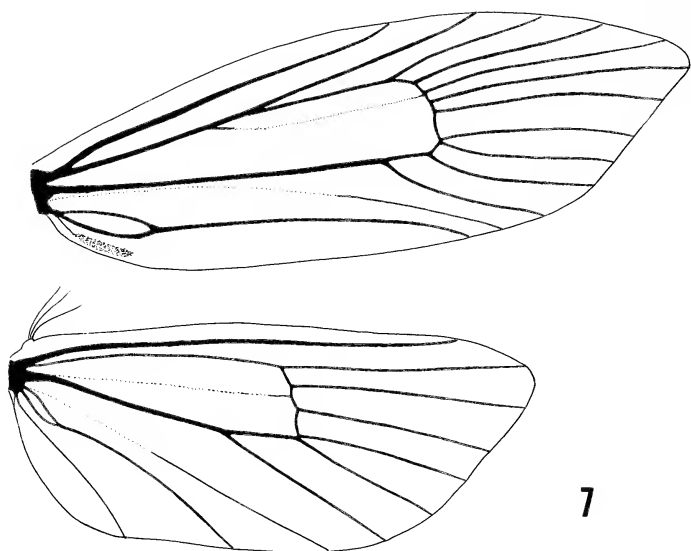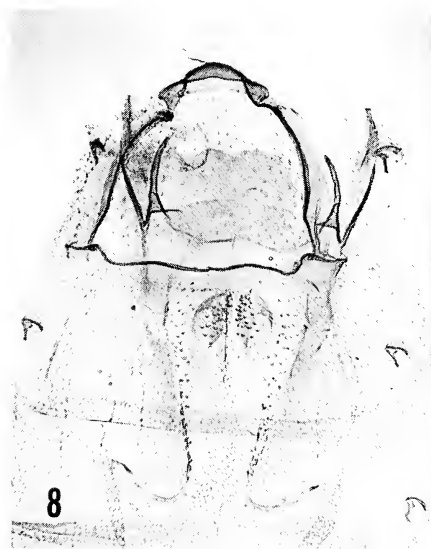British Columbia).

Fig. 7. Wing venation of *Ellabella editha* Busck, ♀ (USNM slide 77374, British Columbia).

Figs. 8-9. Abdominal details of *Ellabella editha* Busck: 8, abdominal articulation and anterior coremata of male (coremata hairs removed) (USNM slide 77117, South Dakota); 9, posterior coremata of male (USNM slide 77116, British Columbia).

spines.

Immature Stages. Larvae bisetose (rarely trisetose); leaf rollers on new foliage (the description is the subject of the following paper by J. De Benedictis).

Distribution. China (Yunnan): western United States and Canada.

Remarks. There are no close relatives of *Ellabella* known and, as noted previously, it remains unclear if *Araeolepia* actually belongs in the same family as a relative of *Ellabella*. The genitalia of *Araeolepia* have superficial similarity to *Ellabella* but other characters relate the genus, to Plutellidae. There may be some relation of *Ellabella* to *Lotisma* but the two genera do not appear very closely related. *Spilogenes* was described as a monobasic genus from China but the morphological features of this genus, including wing venation, head morphology, and genitalic morphology, clearly show relationship to-other *Ellabella*.

Other species of *Ellabella*, in addition to the five known thus far, may yet be found in east Asia and northern Mexico. *Ellabella* moths may tend to remain in the vicinity of their larval hosts, and the consequent colonial nature of such local populations may be a factor in their infrequent collection.

Synopsis of *Ellabella*

	Type-Locality
Ellabella Busck, 1925	
Probolacma Meyrick, 1927	
Spilogenes Meyrick, 1938	
chalazombra (Meyrick, 1938) (*Spilogenes)*	China (Yunnan)
bayensis, n. sp.	USA (California)
johnstoni, n. sp.	USA (Washington)
melanoclista (Meyrick, 1927) (*Probolacma*)	USA (Texas)
editha (Busck, 1925	Canada (British Columbia)

Ellabella chalazombra (Meyrick)

Spilogenes chalazombra Meyrick, 1938:19.

Ellabella chalazombra (Meyrick).-Heppner, 1978:50.

The large, broad gnathos arms in the male genitalia and the very long ductus bursae in the female genitalia will easily distinguish this species from other *Ellabella*. The wing maculation is the most distinctive in the genus.

Forewing length: 10-11 mm (♂); 10.5 mm (♀). **Male.—Head:** vertex dark brown, with yellow-tan scales on lateral areas posterior to antennae and on relatively smooth frons; antenna light tan; labial palpus buff with whitish tan on

mesal side; labial palpus with long slightly curved median segment (3x length of short apical segment). **Thorax:** patagia and dorsum of thorax white, with dark brown spots on anterior ends of patagia; legs buff; venter mostly white, with buff mixed in. **Forewing** (Figure 10): basal half of wing white-tan-irrorated with brown spots along radius and near anal margin and tawny suffusion over dorsal half; dark brown at mid-wing from costal margin diagonally to wing center, then narrowing to CuP fold; dark brown area irrorated with orange-brown scales; dark brown spot of cubitus at ⅓ from wing base; apical ⅓ of wing with 3 dark brown dashed streaks toward apex from mid-wing area; tan with white suffused line distad of mid-wing dark brown area and between brown markings near termen; orange-brown suffusion at end of discal cell and dark brown spot on cubitus at ⅔ from wing base; apical area along costal margin with 3 brown marks; termen with 5 dark brown marks situated between median and cubital veins, with white spots splitting each mark; fringe brown and white; venter gray-brown. **Hindwing:** uniform gray-brown; venter similar; fringe brown and white. **Abdomen:** buff dorsally and somewhat whitish ventrally. Males with small posterior coremata in small pouches with pouch borders small. **Male genitalia** (Figure 22): uncus a long finger-like projection with a widened base having numerous setae laterally on base; gnathos a pair of broad, flat arms, fused at apex as a densely spined area; tegumen simple, widening from uncus base to valval joints; vinculum quadrate; valvae relatively simple, elongate, with rounded and somewhat membranous setaceous distal ends; valvae merging to strong transtilla with pointed ends not entirely fused at center; anellus V-shaped, narrow with pointed distal ends; aedeagus (Fig. 23) straight, with phallobase and apical projection; cornutus a small blade-like structure.

Female (Figure 11).—Wing pattern and other coloration the same as in the male, only with white somewhat more pronounced on basal ½ of wing near anal margin. **Female genitalia** (Figure 34): ovipositor of average length, with setaceous papilla analis; posterior apophyses longer than anterior apophyses, both very stout; anterior apophyses forming ventral triangular sternal plate not quite fused medially; ostium (Fig. 35) membranous, leading to sclerotized half-ring just anterior to it and at juncture with ductus seminalis; ductus bursae twice length of ovipositor, membranous and relatively narrow; bursa copulatrix ovate; signum a small ventral rugose, flat plate.

Immature Stages. Unknown.

Host. Unknown.

Distribution. China: Yunnan.

Flight Period. June-July.

Type. Lectotype ♂ (BMNH). Likiang, Yunnan, China, VI-VII, 2800-3200 m. (lectotype designated by Clarke, [1965]:384).

Material Examined.(8♂, 1♀). China: Yunnan. Likiang, VI-1934 (♂ - USNM; 2♂ - BMNH), H. Hoene; 11-VI-1-VII-1934 (5♂, 1♀), H. Hoene, 2800-3200 m (MGAB) [all paralectotypes].

Remarks. *Ellabella chalazombra* has been collected only once at one site in Yunnan, China. The shaded area of Figure 2 may represent the possible total distribution of *E. chalazombra*, inasmuch as the site is situated within the broadleaf forest delimited on the map where possible *Mahonia* hosts also occur.

The reduced development of the posterior coremata in *E. chalazombra*

may indicate that this species is the most primitive species of the genus. A species of *Anchinia* (Oecophoridae) in China is superficially very similar to *E. chalazombra* in wing maculation, but other characters will easily distinguish the two species.

Ellabella bayensis Heppner, n. sp.

This new species is one of three North American *Ellabella* with a small scleroized collar on the female genital ductus bursae. The male has anellus appendages with rounded ends. The wing maculation is distinctive in having the entire forewing base tan-white, not just the costal half as in the other North American species.

Forewing length: 8.2-11.0 mm ($\circ$); 8.8-10.8 mm (φ) [one dwarf at 6.5 mm]. **Male.—Head:** vertex tan mixed with brown, tan laterally; frons smooth scaled, silvery tan; antenna tan; labial palpus brown and tan mottled on sides, tan on mesal side, with median segment having scales making it appear twice actual width; median segment of labial palpus slightly curved and about 2.5-3x length of small apical segment. **Thorax:** tan mixed with white and brown; patagia pale tan, with dark brown anterior border, followed by mostly white; venter mostly white; legs brown and tan, with brown and white on tarsal segments. **Forewing** (Figure 12): brown irrorated with tan and white scales as in *E. chalazombra*; basal ½ of wing with more white evident, somewhat surrounding dark brown mark from costa to CuP fold, sometimes somewhat split centrally by buff area; 4-5 dark brown costal marks on apical half of wing, with spotted streaks along radial veins more or less prominent; chocolate brown marks on basal ⅓ on Rs and at end of cell by M_1 and by CuA_1 and CuA_2 (or dark brown vertical line at end of cell, with a small dark brown spot between it and mid-wing large dark spot); termen with spotted dark brown lines between veins and veins highlighted by brown lines; fringe tan; venter gray-dark brown. **Hindwing:** uniformly pale gray-tan; fringe same; venter dark gray-tan. **Abdomen:** tan; venter tan mixed with white; posterior coremata in male long, with pouch borders larger than in *E. editha* and with long central notch. **Male genitalia** (Figure 24): as in *E. chalazombra*, with elongated uncus on widened setaceous base; gnathos as a pair of stout, flattened appendages less wide than in *E. chalazombra*; valvae simple, elongate-oblong, setaceous with rounded distal ends, with sacculus having small sharp projection which is separated from a mid-valval slightly carinate ridge; anellus U-shaped with distal appendages rounded and broad; aedeagus (Fig. 25) slightly angulate, with half-phallobase; cornutus a curved spine.

Female (Figure 13).—Same as male. **Female genitalia** (Figure 36): ovipositor of average length, with setaceous papilla analis; apophyses with posterior pair twice length of anterior pair; sternal plate of segment 8 with prominent central point; ostium (Fig. 37) a wide membranous funnel, relatively short before terminating at sclerotized collar on ductus bursae posterior to entrance of ductus seminalis; ductus bursae subequal in length to corpus bursae, membranous and slightly convoluted; corpus bursae ovate, with small rugose plate as signum.

Immature Stages. Larvae and pupae known; foliage feeders from silk-tied shelters (description in following paper by J. De Benedictis).

Host. *Mahonia pinnata* (Lagasca) Fedde (Berberidaceae).

Distribution. California (San Mateo Co.).

Flight period. January-March (rearing records); March (wild collected moth).

Type. Holotype ♂ (UCB). San Bruno Mt., San Mateo Co., California, larvae 21-IV-1981, emerged 8-II-1982 ex *Mahonia pinnata* (J. Powell lot 81D41), J. A. De Benedictis coll. (Holotype deposited with CAS on indefinite loan from UCB).

Material examined. Paratypes: (1♂, 11♀). USA: California. San Mateo Co.: San Bruno Mt., 2-III-1967 (1♂), P.A. Opler (UCB); larvae 21-IV-1981, (8♂, 10♀), emerged 5-I-4-III-1982 (also 6 from 20-VI to 27-XII-1981) ex *Mahonia pinnata* (J. Powell lot 81D41) (UCB); larvae 15-IV-1981 (2♂, 1♀)k, emerged 15-XII-1981 and 11-14-I-1982 ex *Mahonia pinnata* (J. Powell lot 81D36) (UCB).

Remarks. This California species is very closely related to *Ellabella johnstoni*, n. sp., from Washington state. *Ellabella bayensis* is distinct in wing pattern and genitalic details, and the range of the known host also appears to indicate that the two species are distinct. The known range of *Mahonia pinnata* is shown on Figure 1 as a delimited area in California to extreme southern Oregon (Josephine Co.) and extending to the Mexican border. It is probable that both the host and the moth also occur south of the border in Baja California. Only a single generation per year (January-March) is confirmed thus far although laboratory rearings have produced moth emergences from June until December as well.

Ellabella johnstoni Heppner, n. sp.

A species from Washington state that is noticeably larger than other *Ellabella*. The species has a dark forewing base, but other maculation is similar to *E. bayensis*.

Forewing length. 11.0-13.0 mm (♂); 11.5 mm (♀).

Male.—Head: vertex as in *E. bayensis* with tan and brown; frons brown to dark brown; labial palpus brown and tan, mostly tan on mesal side; antenna tan and brown; labial palpus with median segment long and straight (ca. 3x small apical segment), with dorsal scale tuft. **Thorax:** brown and tan mixed, with median dark brown tuft merged laterally to form dark line across patagia; posterior of thorax dorsum tan and white; patagia with posterior end tan and white; venter mostly white, with some tan; legs brown and tan, white on mesal sides. **Forewing** (Figure 14)**:** ground color tan with dark brown area on most of mid-wing area from CuP fold to costal margin; a tan area (with some chocolate brown scales) at mid-wing, with a central dark brown spot or short line; another dark brown line at end of discal cell (vertical) and a small dark brown spot (irrorated white) along cubitus basad of cell end line; 4 costal dark brown marks (irrorated with white) on apical ¼; intervein spaces along termen with dark brown lines, irrorated with some white; fringe brown and white; venter gray brown. **Hindwing:** uniform pale gray-tan; venter gray brown; fringe tan and white. **Abdomen:** brown and tan; venter somewhat lighter; male posterior coremata longer and thinner than those of *E. bayensis*, otherwise with similar pouch border shape. **Male genitalia** (Figure 26)**:** very similar to *E. bayensis* but about 30% larger; gnathos arms somewhat more stout; valvae more oblong and rounded on distal ends; valval saccular projection rounded and carinate ridge almost absent; annelus appendages similar to *E. bayensis* but with distal ends blunted to slight point; aedeagus (Fig. 27) with cornutus relatively straight.

Female (Figure 15). Similar to male. **Female genitalia** (Figure 38): similar to *E.*

bayensis but in general larger, with anterior apophyses somewhat longer; sternal plate (Fig. 39) of segment 8 with base curved more toward central projection than the almost abrupt juncture in *E. bayensis.*

Immature stages. Unknown.

Host. Unknown.

Distribution. Washington.

Flight period. April-May.

Type. Holotype ♂ (CNC). Stimson Cr., Mason Co., Washington, 17-IV-1949, E.C. Johnston.

Material examined. (3♀). USA: Washington. Mason Co.: Stimson Cr., 17-IV-1949 (1♀), 22-V-1949 (1♀), E.C. Johnston (CNC). Whatcom Co.: Bellingham, 14-IV-1927 (1♀), J.F.G. Clarke (USNM) [all paratypes].

Remarks. This species of *Ellabella* occurs near localities from which *Ellabella editha* was described, yet has been very rarely collected. It is noticeably larger than other *Ellabella* but is closely related to *E. bayensis.* There also is an apparent close relationship with *Ellabella melanoclista* (Meyrick) in some of the wing markings and some genital features, such as the valval carinae and annellus of the male.

The species is named in honor of E. C. Johnston, who collected many unusual moths in the Pacific Northwest.

Ellabella melanoclista (Meyrick)

Probolacma melanoclista Meyrick, 1927:362.

Ellabella melanoclista (Meyrick).—Clarke, [1965]:418.

A dark southwestern species, with male genitalia having truncated valvae.

Forewing length. 9.6-11.2 mm (♂), 10.0-11.2 mm (♀).

Male.—Head: vertex and frons dark brown mixed with black and white; antenna dark brown; labial palpus dark brown, with white mixed in on both sides or lighter on mesal side; labial palpus with median segment having apical tuft and about 2.5x length of small apical segment. **Thorax:** dark brown mixed with black, with scales white-tipped; patagia same; venter white; legs dark brown to black. **Forewing** (Figure 16): dark brown to black irrorated with some white near base, around the three mid-wing black marks (as in *E. johnstoni*), and on apical ¼; apical ¼ sometimes with veins highlighted by brown or white irrorations; termen marks indistinct, sometimes as broken subterminal lines; fringe brown and white; venter dark gray brown. **Hindwing:** uniform pale gray-brown; fringe brown and white; venter gray brown. **Abdomen:** gray-brown; venter lighter; male posterior coremata long and large, with pouch borders not as convex anteriorly as in *E. johnstoni* but with similar central notch. **Male genitalia** (Figure 28): similar to *E. bayensis* but smaller, with shorter uncus; valvae distinctly truncated apically, with saccular projections rounded and valval carinate ridge very slight; annellus appendages similar to *E. johnstoni* but somewhat more pointed; aedeagus (Fig. 29) with curved cornutus.

Female (Figure 17). Similar to male but sometimes with more extensive white suffusion over wings. **Female genitalia** (Figure 40): similar to *E. bayensis* and *E. johnstoni* but smaller overall yet with proportionally larger corpus bursae; signum (Fig. 42) somewhat larger and more concave.

Immature stages. Unknown.

Host. Unknown.

Distribution. Arizona to Texas.

Flight period. March-May.

Type. Holotype ♀ (BMNH). Alpine, Brewster Co., Texas, IV-1926, 5000 ft. [1520 m].

Material examined. (3♂, 3♀). USA: Arizona. Yavapai Co.: Prescott, 30-III-1971 (1♀), 7-IV-1970 (1♂), L.M. Martin (UCB); 5 mi. N. Prescott, 11-IV-1974 (1♂, LACM), 2-V-1974 (1♂, LACM), 9-V-1974 (1♀, UCB), L.M. Martin, 5450 ft. [1680 m]. Texas. Kerr Co.: Kerrville, III-1907 (1♀), H. Lacy (USNM).

Remarks. *Ellabella melanoclista* is another rarely collected species that only recently has been found more frequently in Arizona. This species may well also be found in adjacent upland areas of juniper woodland in northern Mexico. The moths appear somewhat like melanic *E. johnstoni* but the genitalia are noticeably distinct. The female from Kerrville appears to be *E. melanoclista* inasmuch as the genitalia do not show the long ductus bursae collar of *E. editha*, yet the wing maculation has much more white than is typical (this may be due to the removal of darker scales following prolonged flight).

Ellabella editha Busck

Ellabella editha Busck, 1925:48.

This widespread species is most readily distinguished by the more evident forewing scale tufts and in the genitalia. The male genitalia show anellus appendages with truncated distal ends and mesal points, while female genitalia show a long sclerotized collar on the ductus bursae.

Forewing length. 9.5-11.0 mm (♂), 8.0-11.5 mm (♀).

Male.—Head: similar to *E. bayensis*, with vertex and frons tan and brown; antenna white and tan; labial palpus brown mixed with white, mostly white on mesal side; median segment of labial palpus long (ca. 3x length of short apical segment) and straight. **Thorax:** brown and white, with median tuft and posterior tuft of dark brown; patagia brown and white, with more or less distinct median line of dark brown; venter white; legs white and brown with some dark brown areas. **Forewing** (Figure 18): similar to *E. bayensis*, with gray-brown irrorated with white and more extensive white on apical ¼ and basal ⅓ along costal margin; a large mid-wing area of dark brown mixed with tan, with chocolate-brown along radius and cubitus; 2-3 black tufted spots in cell separated by dark brown mixed with tan or white; a small dark brown spot between basal two tufts but indistinct; white line at end of cell and bordering distal of black spots vertically; apical ¼ irrorated with white over gray-tan, with few distinct marks except for two parallel subterminal lines (usually irregular) of brown and tan but these often indistinct; streaks of brown and tan sometimes distinct on apical ¼ (Fig. 20); fringe gray-brown and white; venter brown. **Hindwing:** uniform gray-brown; fringe brown and white; venter darker. **Abdomen:** tan and brown; venter somewhat lighter; male posterior coremata (Fig. 9) very short, with pouch borders having small median notch. **Male genitalia** (Figures 30, 32): similar to *E. bayensis* but with uncus shorter; gnathos with lateral

arms narrower and distal spined pads wider; valvae elongate, with distal ends not enlarged, sometimes narrower than middle area (Fig. 32); valval saccular projection carinate and central carinate ridge elongated; annellus with widely separated appendages, broader than in *E. bayensis*, and with truncated ends with a sharp mesal point; aedeagus angulate with small phallobase; cornutus a curved spine.

Female (Figures 19, 21). Similar to male but tending to have more white on head, body and wings. **Female genitalia** (Figure 43): similar to *E. bayensis* and other North American species but with sternal plate of segment 8 having curved base; ductus bursae with elongated sclerotized collar (ca. 3x longer than in other species); signum (Fig. 44) subovate, with rugose spines more fused than in other species; corpus bursae noticeably larger than in other species.

Immature stages. Unknown.

Host. Unknown (possibly *Mahonia repens* (Lindl.) G. Don which is the only *Mahonia* in Alberta).

Distribution. Canada (Alberta and British Columbia); USA (Arizona, Colorado, New Mexico, Oregon, South Dakota, Texas, Utah, Washington, Wyoming).

Flight period. May-August (most records for June-July).

Type. Holotype ♀ (USNM). Saanichton, Vancouver Id., British Columbia, Canada, 10-VI-1922, J.G. Colville.
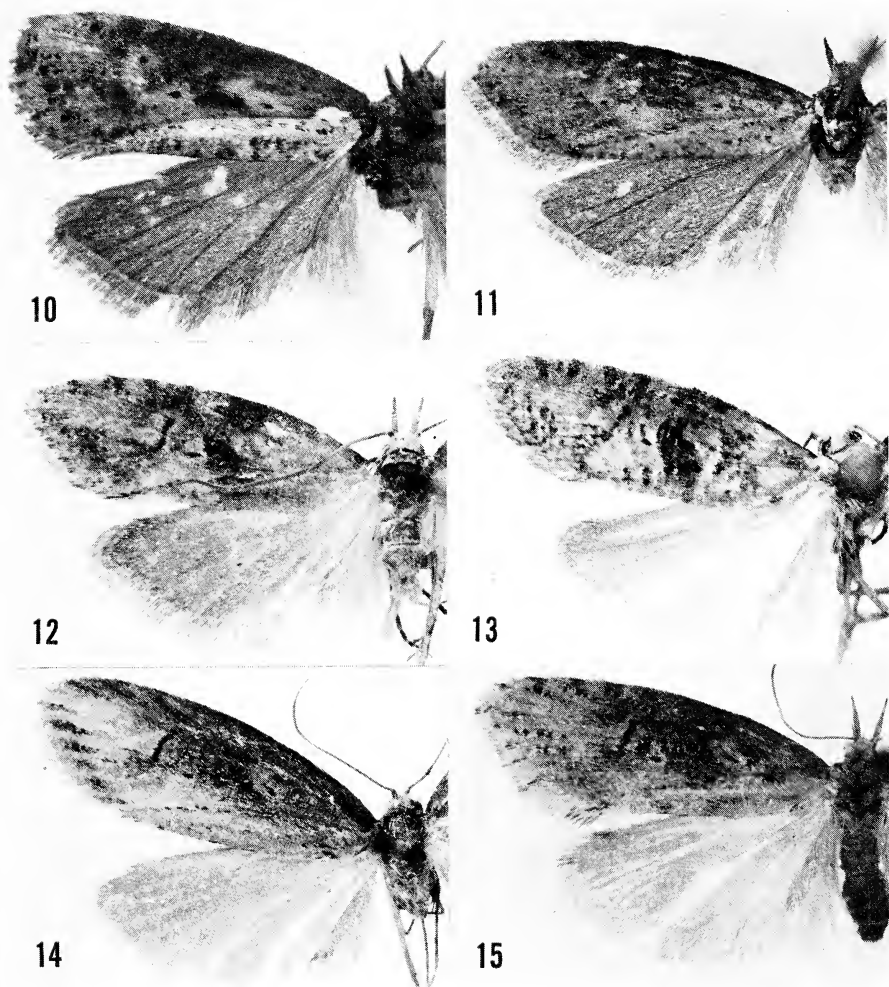
Material examined. (44♂, 26♀). Canada: Alberta. Waterton Lakes, 8-VII-1923 (1♂), 13-VII-1923 (1♀ paratype), 24-VII-1923 (1♀), J.H. McDunnough (CNC). British Columbia. Kaslo, 4-VI-1904 (1♂, ANSP), 12-VI-1906 (1♂, AMNH), VII-1924 (1♂, USNM), J.W. Cockle. Keremeos, 9-VI-1935 (1♀, UCB), 30-VI-1936 (1♀, UCB; 1♂, CNC), A.N. Gartrell. Penticton, 25-VI-1935 (1♀), A.N. Gartrell (CNC). Vancouver Id.: Quamichan Lk., [no date] (2♂ paratypes), 27-V-1902 (1♂), 3-VI-1914 (1♂), E.H. Blackmore (USNM); [no date] (1♂ paratype), E.H. Blackmore (UCB); Saanichton, 22-VI-1922 (1♀ paratype), E.H. Blackmore (USNM); Shawnigan, 23-VI-1925 (1♀), E.H. Blackmore (USNM); Victoria, 28-VI-1921 (1♀), W.R. Carter (USNM); Brentwood, 30-VI-1923, (1♂), E.H. Blackmore (USNM); Mt. Newton, 2-VIII-1924 (1♀), E.H. Blackmore (UCB); [no locality], 1-VI-1905 (1♂), 16-VI-1909 (1♂), E.H. Blackmore (USNM).

USA: Arizona. Coconino Co.: Fort Valley, 7½ mi. NW Flagstaff, 20-VI-1961 (1♂), 25-VII-1961 (1♂), 13-VIII-1961 (1♂), 17-VIII-1961 (1♂), 18-VIII-1961 (1♂), R.W. Hodges, 7350 ft. [2275 m], (USNM); 52 mi. N. Williams, 26-VIII-1968 (2♀), C. Slobodchikoff (UCB). Mohave Co.: [no locality], 1-7-VIII (1♀), [no coll.] (USNM). Yavapai Co.: 5 mi. N. Prescott, 4-VI-1973 (1♂), L.M. Martin, 5450 ft. [1680 m] (LACM). Colorado. Jackson Co.: Gould, 11-VIII-1956 (1♂), F. & P. Rindge, 9000 ft. [2750 m], (AMNH). New Mexico. Colfax Co.: Cimarron Cyn., Sangre de Cristo Mts., 6-VII-1962 (1♂), E. & I. Munroe, 7900 ft. [2400 m] (UCB). Lincoln Co.: Nogal Lk. Cpgd., 4 mi. SE. Nogal, 4-VII-1977 (1♀), J.B. Heppner, 7000 ft. [2135 m], (JBH). Sandoval Co.: Horshoe Spgs. Camp, 2 mi. W. La Cueva, 28-VII-1961 (1♀), F., P. & J. Rindge, 7900 ft. [2400 m] (AMNH). Oregon. Douglas Co.: Whitehorse Falls Cpgd., 12 mi. NW. Diamond Lk., 30-VII-1982 (2♂), J. De Benedictis & J. A. Powell, 3800 ft. [1160 m], (UCB). Lane Co.: Alder Spgs. Cpgd., 11 air km. E. Belknap, 31-VII-1982 (3♂), J. De Benedictis & J. A. Powell, 3500 ft. [1070 m] (UCB). South Dakota. Pennington Co.: Hardy Work Ctr., 20-VII-1965 (3♂), 21-VII-1965 (2♂), R.W. Hodges (USNM). Texas: Culberson Co.: Sierra Diablo, 20 mi. NW. Van Horn, 27-V-1973 (2♀), 30-V-1973 (1♀), R.W. Hodges, 6000 ft. [1825

m] (USNM). Utah. Garfield Co.: Blue Spruce Camp, 18 mi. N. Escalante, 2-VII-1963 (1♂), F., P. & M. Rindge, 8000 ft. [2415 m] (AMNH); Red Cyn. Camp, 11 mi. SE. Panguitch, 31-VII-1965 (1♀), F., P. & M. Rindge, 7100 ft. [2150 m] (AMNH). Provo Co.: Provo, 19-VII-1909 (1♂), T. Spalding (AMNH). Sanpete Co.: Ephraim Cyn., Grt. Basin Exp. Sta., 19-VII-1981 (1♀), 21-23-VII-1981 (1♂), R.W. Hodges, 8850 ft. [2700 m] (USNM). Tooele Co.: Loop Camp, 13 mi. SW. Grantsville, 1-VII-1960 (1♂, 1♀), F., P. & B. Rindge, 7400 ft. [2250 m] (AMNH). Washington. Jefferson Co.: Rosemary Inn, Olympic Mts., 21-VI-1939 (1♀, UCB), 22-VI-1939 (1♂, AMNH), 28-VII-1939 (1♂, 1♀, USNM), G.H. & J.L. Sperry. Wyoming. Crook Co.: Reuter Cyn. Camp, 5 mi. N. Sundance, 11-VII-1962 (1♂), F., P. & M. Rindge, 5900 ft. [1790 m] (AMNH). Fremont Co.: Louis Lk., 28 mi. SW. Lander, 30-VII-1962 (1♂), 1-VIII-1962 (1♂, 1♀), 2-VIII-1962 (1♂), 4-VIII-1962 (1♂, 1♀), 5-VIII-1962 (1♂), F., P. & M. Rindge, 8600 ft. [2625 m] (AMNH). Sublette Co.: Lower Green R. Lk., Wing River Range, 30-VII-1953 (1♀), F. & P. Rindge, 8000 ft. [2435 m] (AMNH).

Remarks. *Ellabella editha* is the type-species of the genus and also the most widespread. Although ranging from British Columbia and Alberta to Arizona and Texas, it is uncertain whether it occurs in Mexico. A possible host, *Mahonia repens*, is not known to occur south of central Arizona and southern New Mexico. Both *Ellabella johnstoni* and *E. melanoclista* have earlier flight periods than most records indicate for *E. editha*, with May being the only month of possible overlap in areas where any two of the species occur. In Prescott, Arizona, *E. melanoclista* flies from March to April, however, and *E. editha* has been recorded there only in June. The genital differences between the two species would not make it possible to consider them only seasonal forms.

Figs. 10-15. Adults of *Ellabella*: 10, *E. chalazombra* (Meyrick), ♂ paralecto-
type, Yunnan, China (USNM); 11, same, ♀ (MGAB); 11, *E.
bayensis*, n. sp., ♂ paratype, California (UCB); 12, same, ♀
paratype (UCB); 13, *E. johnstoni*, n. sp., ♂ holotype, Washington
(CNC); 14, same, ♀ (USNM).
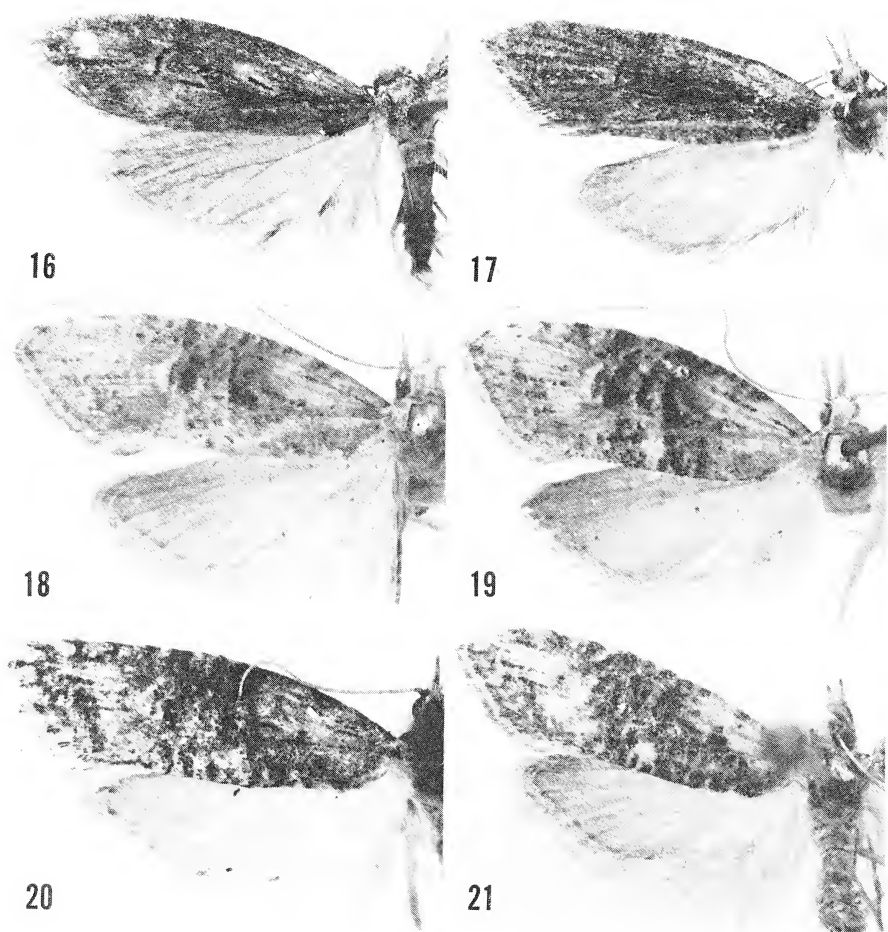
Figs. 16-21. Adults of *Eliabella*: 16, *E. melanoclista* (Meyrick), ♂, Arizona (UCB); 17, same, ♀ (UCB); 18, *E. editha* Busck, ♂, British Columbia (USNM); 19, same, ♀ holotype (USNM); 20, same, ♂, Arizona (USNM); 21, same, ♀, Texas (USNM).
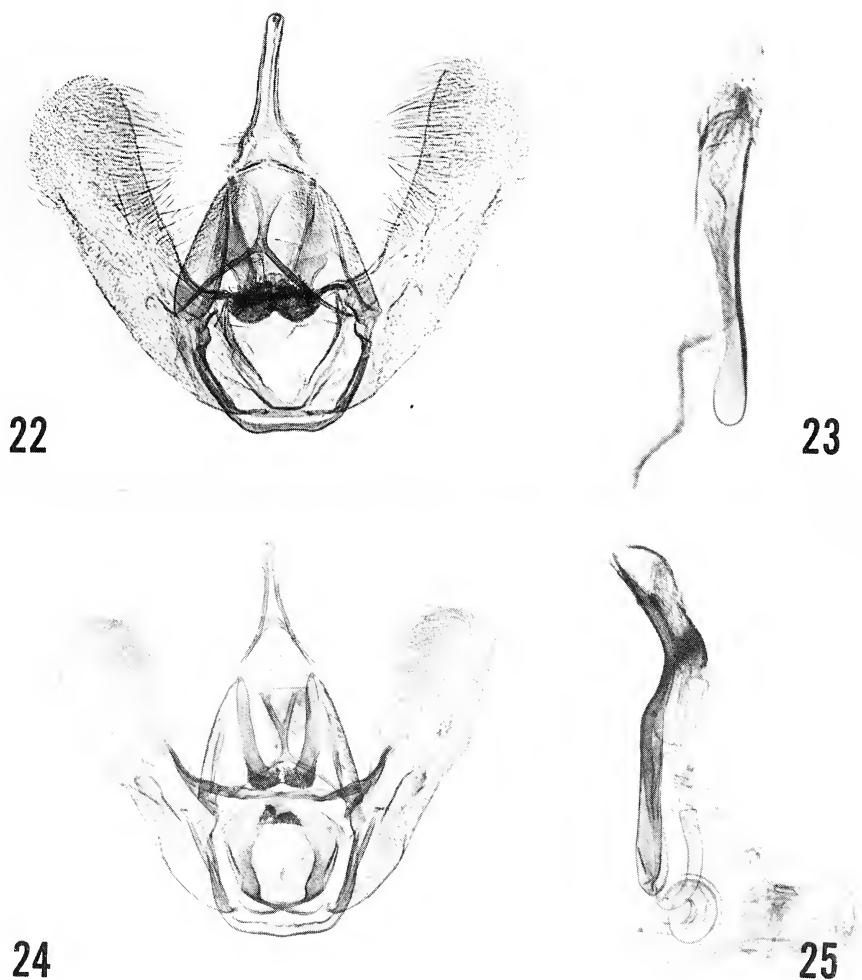
Figs. 22-25. Male genitalia of *Ellabella*: 22, *E. chalazombra* (Meyrick), ♂ paralectotype, Yunnan, China (USNM slide 7756); 23, same, detail of aedeagus (enlarged); 24, *E. bayensis*, n. sp., ♂ holotype (UCB), California (JBH slide 1721); 25, same, detail of aedeagus (enlarged).
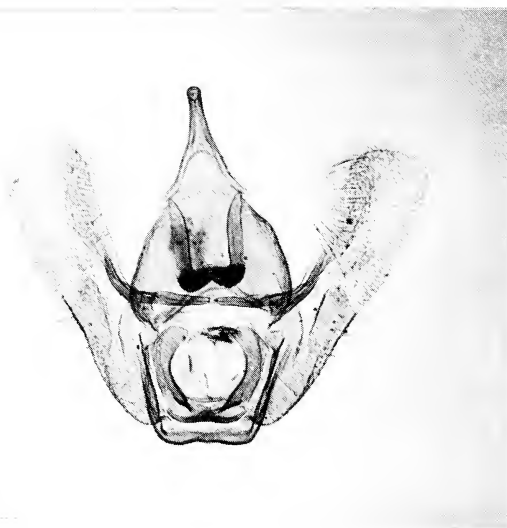
Figs. 26-29.   Male genitalia of *Ellabella*: 26, *E. johnstoni*, n. sp., ♂ holotype
(CNC), Washington (JBH slide 1672); 27, same, detail of
aedeagus (enlarged); 28, *E. melanoclista* (Meyrick), Arizona
(JBH slide 1677); 29, same, detail of aedeagus (enlarged).
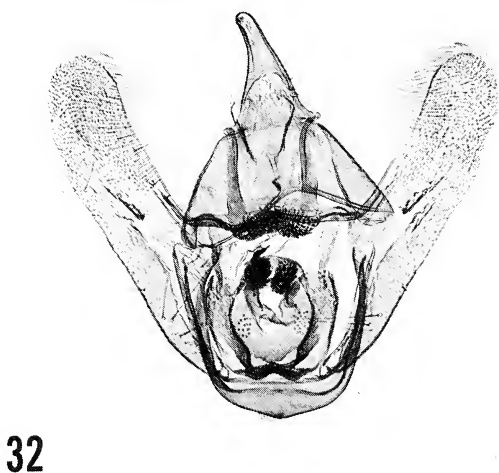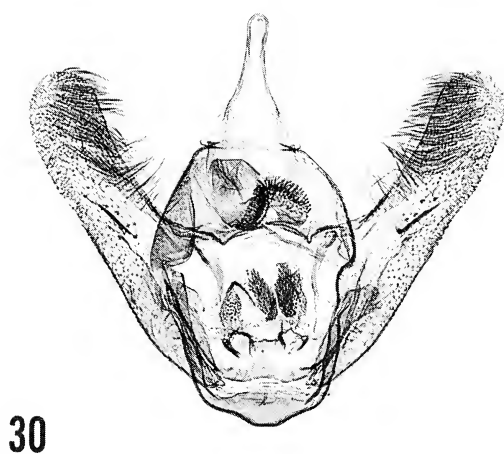
Figs. 30-33. Male genitalia of *Ellabella*: 30, *E. editha* Busck, British Columbia (USNM slide 77116); 31, same detail of aedeagus (enlarged); 32, *E. editha*, Arizona (USNM slide 77758); 33, same, detail of aedeagus (enlarged).
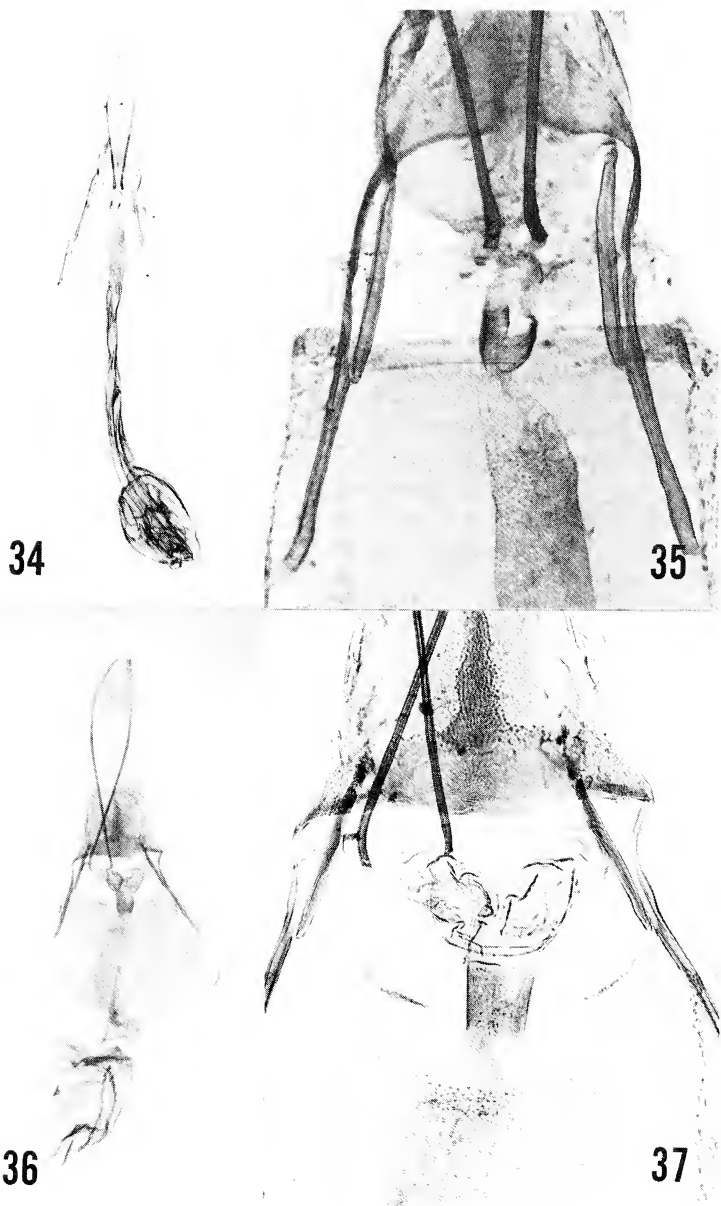
Figs. 34-37. Female genitalia of *Ellabella*: 34, *E. chalazombra* (Meyrick), ♀
paralectotype (MGAB), Yunnan, China (JBH 1646); 35, same,
detail of ostium; 36, *E. bayensis*, n. sp., ♀ paratype (UCB),
California (JBH slide 1723); 37, same, detail of ostium.
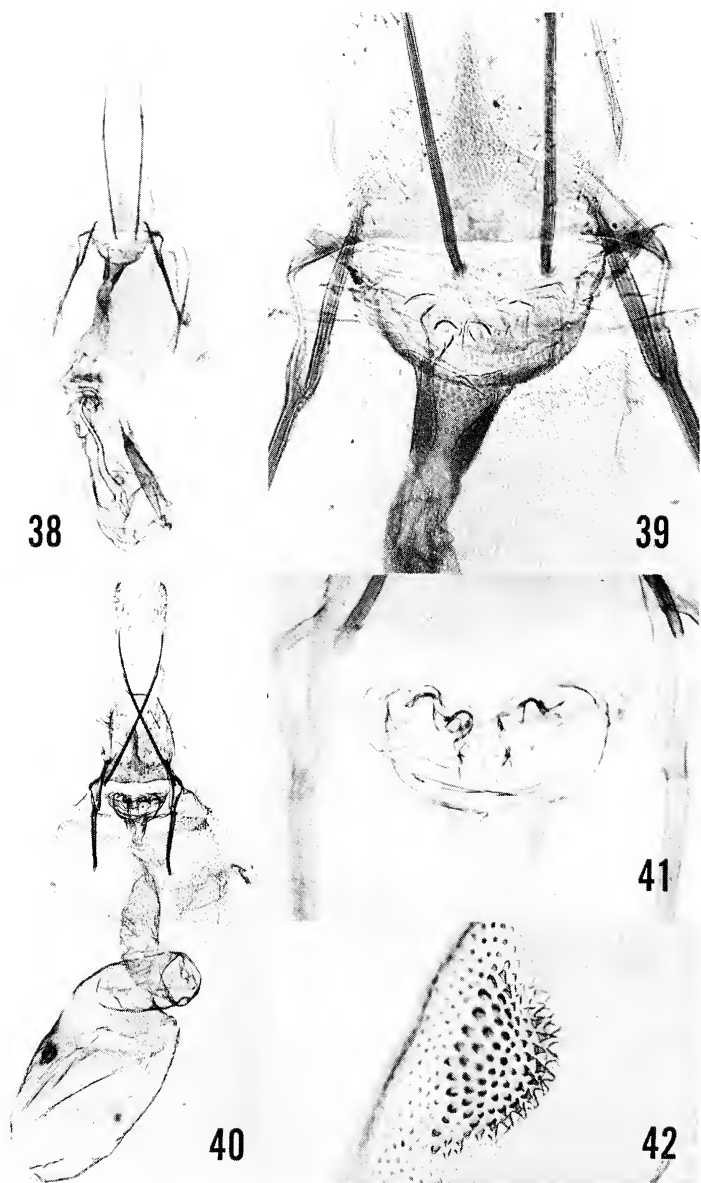
Figs. 38-42. Female genitalia of *Ellabella*: 38, *E. johnstoni*, n. sp., ♀ paratype, Washington (USNM slide 77757); 39, same, detail of ostium; 40, *E. melanoclista* (Meyrick), ♀ holotype (BMNH), Texas (after Clarke, [1965]:418); 41, same, detail of ostium; 42, same, detail of signum.
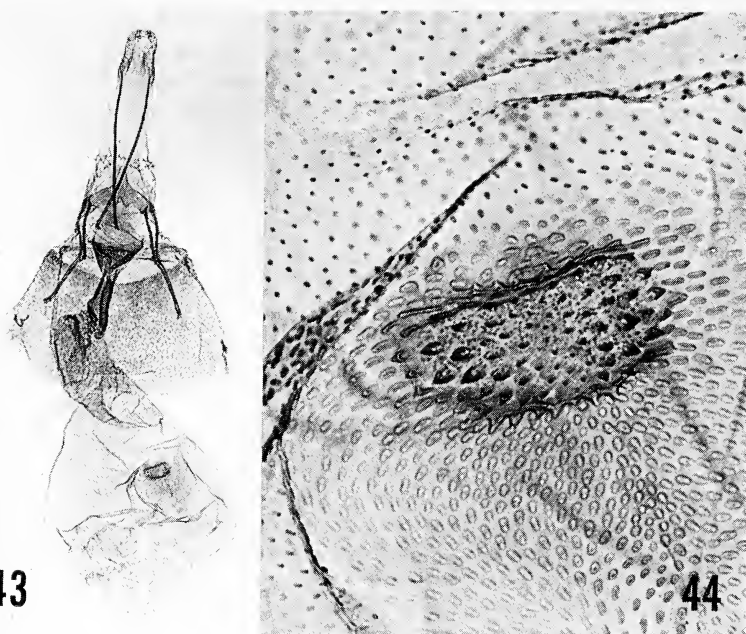
Figs. 43-44. Female genitalia of *Ellabell editha* Busck: 43, British Columbia (USNM slide 77203); 44, same, detail of signum.

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On the Taxonomic Position of *Ellabella* Busck, with Descriptions of the Larva and Pupa of *E. bayensis* (Lepidoptera: Copromorphidae)

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Abstract. The final instar larva, pupa, and some biological observations of *Ellabella bayensis* Heppner are described. The larval host is *Mahonia pinnata* (Lagasca) Fedde (Berberidaceae). Larval and pupal characters indicate that the genus *Ellabella* Busck, which has been placed in four families in three superfamilies since 1925, is in Copromorphidae. Although some characters vary from other Copromorphidae, others, especially chaetotaxy, support the transfer of *Ellabella* to that family.

Introduction

Busck (1925) described the genus and species *Ellabella editha* from moths collected in British Columbia and Alberta. He placed the genus in Glyphipterigidae (*auctorum*) based upon similarities in wing venation to those of *Lotisma* Busck and *Araeolepia* Walsingham. This treatment was followed by McDunnough (1939) even though Fletcher (1929) placed *Ellabella* and *Lotisma* in Yponomeutidae and *Araeolepia* in Plutellidae. Clarke (1955) transferred *Ellabella* to Ethmiidae following Meyrick (1927), who considered the genus (as *Probolacma* Meyrick) and *Lotisma* to be near *Ethmia* Huebner. However, Powell (1973) determined that characters of *Lotisma* and *Ellabella* were not gelechioid and removed both genera from Ethmiidae. Heppner (1978) transferred *Ellabella* and *Araeolepia* to Plutellidae and *Lotisma* to Copromorphidae in order to maintain consistency among the Glyphipterigidae (*sens. str.*).

Except in the case of *Lotisma*, Heppner's decisions were made without knowledge of the early stages. In April, 1981, I collected several larvae of a then undescribed *Ellabella* species on coastal barberry, *Mahonia pinnata* (Lagasca) Fedde (Berberidaceae). Heppner (1984) described this species as *E. bayensis* and suggested that the genus is likely in Copromorphidae. Larval and pupal characters indicate that *Ellabella* should not be placed in Plutellidae, and that although some characters are inconsistent with known Copromorphidae, others substantiate its placement in Copromorphidae.

Collection and Rearing Notes

Larvae were collected during April 1981 (J. De Benedictis Lot No. 81105-A and 81111-D) and April 1982 (Lot No. 82099-B and 82106-F) in the county park on San Bruno Mountain, San Mateo County, California. Larvae fed upon *Mahonia pinnata* (Lagasca) Fedde, coastal barberry. Coastal barberry sometimes is used as an ornamental in urban areas but is widespread and presumably native on San Bruno Mountain.

Except for two larvae found feeding in flowers, all larvae fed on new foliage. Old foliage is hard, spiny, and apparently seldom, if ever, fed upon by Lepidoptera larvae.

All but two foliage-feeding *E. bayensis* larvae were found in tightly-rolled new leaves, and both exceptions were smaller larvae. One was between the folded halves of a small leaf; the other was beneath a pad of silk on the underside of a new leaf and appeared to have been parasitized. Rolled shelters are constructed from a single leaf or from two or more overlapping leaves. Edges of the feeding shelter are sealed with a heavy silk seam except for a small opening through which frass is ejected.

Larvae apparently eat only the portion of leaves within the shelter then gnaw their way out to construct a new shelter. In one instance, silk led from an abandoned shelter to a flower cluster, but neither signs of feeding nor the larva were found. However, flower feeding may be more frequent than the two of the more than 50 larvae collected suggest. The yellow and green larvae closely match the flower colors, so larvae are difficult to locate within the flower clusters. On the other hand, larval coloration is a striking contrast to the bright red new leaves of coastal barberry.

Two larvae and a pupa from the 1981 collection and all larvae collected in 1982 were preserved in 95% ethanol after distension by boiling in water. The remainder of the 1981 collections was reared on cut foliage in plastic bags. The collections were housed in a mobile trailer lab with the minimum temperature controlled at approximately 19°C, so developmental times likely were not normal. Bags were inspected almost daily to collect emerging adults and to evert as necessary to release excess moisture.

Beginning in May, fully grown larvae ceased feeding and began constructing cocoons from materials in the rearing bags. Occasionally, they concealed themselves in dry foliage, but most larvae used the underlying paper towels or folds of plastic as the outer surface of the cocoon. Most chewed a semicircle in the paper towel or plastic, folded it over, and tied it with silk to the flat surface. A few sealed the edges of existing folds in the paper towels or plastic bags.

Development could be observed through the translucent plastic. Most larvae remained as prepupae for five or six months, but a few pupated within a week or two after spinning cocoons. Four adults emerged between late June and early July 1981, one emerged in early October, and 25 others emerged between late December 1981 and early March 1982. Pupal cases

remained within the cocoons at eclosion.

Description of Early Stages

Final instar larva (Figures 1-5). **Head** (Figures 3-5): Width 1.31 to 1.47 mm, amber with darker crescent surrounding stemmata 1-5; frontal triangle slightly broader than high, tapering toward apex, extending nearly ¾ to epicranial notch; stemmata 1-6 in nearly evenly spaced semicircle except 5 displaced toward mouth; submental setae on small tubercales on V-shaped pigmented patch (Figure 5).

Body: Robust; distended length 9.2 to 14.3 mm; dorsum olive, occasionally with two indistinct narrow yellow-green longitudinal stripes; lateral and ventral surfaces yellow to yellow-green; one or two pairs or irregularly shaped dark brown blotches per segment in a dorsolateral longitudinal line from the prothorax immediately ventrad of cervical shield to segment A9; a narrow white longitudinal stripe adjacent and ventrad of line of blotches; dorsum exclusive of cervical shield lightly peppered with dark brown from prothorax to A9; unpigmented primary setae only, usually borne individually on small, weakly differentiated, sometimes amber pinnacula; setae relatively short.

Thorax: Cervical shield light to medium amber; prothorax with bisetose pre-spiracular group (L-group); prothoracic L- and SV-groups borne paired on amber pinnacula; prothoracic spiracle approximately twice the diameter of abdominal spiracles.

Abdomen: A1 with trisetose L-group, SV1 and V1 present, SD2 absent; spiracles placed somewhat anteriad near middle of segments, spiracle on A8 somewhat larger than others; A9 lacking D1; anal shield pale amber; prolegs on A3-6 and A10, short, cylindrical; crochets 35 to 44 in nearly uniordinal circle, mesal half of circle biserial, lateral half uniserial, lateral crochets often shorter than mesal (Figure 2).

Discussion: Based upon head capsule widths, 12 of 35 larvae were in the final instar. The remainder were in the penultimate and antepenultimate instars except one which was probably younger. Only the final instar is marked with the dark brown longitudinal lines of blotches and dorsal speckling. Earlier instars also differ in that head capsules and, sometimes, cervical shields are black.

Pupa (Figures 6-7): Pale to deep amber; length 6.9 to 7.1 mm; fusiform; encased in silk-lined cocoon.

Head: Rounded anteriorly; two pair of setae on frons near antennal bases; antennae extending to wing tips near anterior margin of A9, not touching at ventral meson; eyes prominent, separated by relatively broad, somewhat trapezoidal labrum; triangular pilifiers laterad of labrum; labial palpi extending from base of labrum to A2; maxillae broad at base, laterad of labial palpi; haustellum extending nearly to wing tips along ventral meson; trangular maxillary palpi anteriad of tibiae of forelegs.

Thorax: Prothorax and mesothorax with a pair of short fragile setae near wing bases; forelegs laterad of maxillae, extending to A4, femora of forelegs partially visible between maxillae and tibiae of forelegs; mesolegs laterad of forelegs, extending nearly to wing tips; hindlegs concealed behind wings and haustellum except tarsi visible caudad of haustellum; wings long, extending to A9, not touching at ventral meson, hindwings visible as narrow strips dorsad of forewings; appendages caudad of A4 not touching abdomen.
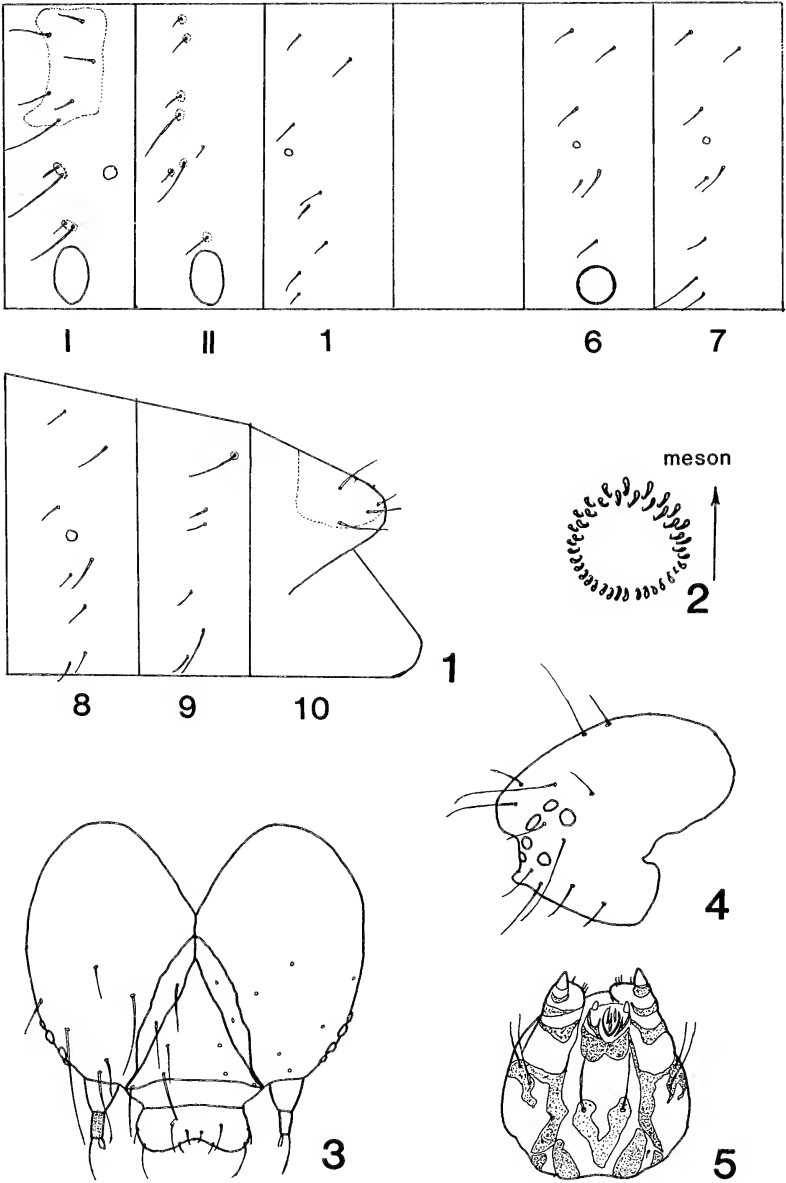
Figs. 1-5. Larva. Fig. 1: Setal map. Roman numerals denote thoracic segments; arabic numbers denote abdominal segments. Fig. 2: Map of crochets on prolegs of A3-6. Fig. 3: Frontal view of head. Fig. 4: Lateral view of head. Fig. 5: Labium and maxillae.
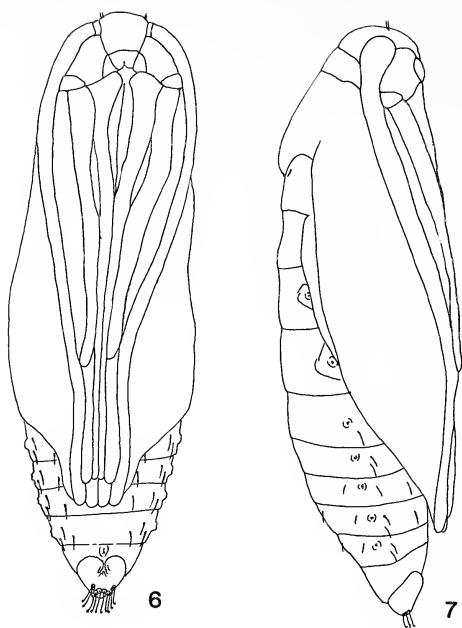
Figs. 6 & 7. Pupa. Fig. 6: Ventral aspect. Fig. 7: Lateral aspect.

Abdomen: Spiracles protruding, those on A2 and 3 protrude from triangular elevated lobes; segments A5, 6, and 7, and 8-10, as a unit, moveable; abdominal setae short, fragile; one pair of dorsal setae on A7 and 8 only; A5-8 with three pairs of setae in double row ventrad of spiracles and single row approximately midway between spiracles and ventral meson; A4 with seta posterioventrad of each spiracle; A3-8 with a pair of setae in single row anteriodorsad of spiracles; cremaster of ten setae.

Discussion: In the lab, larvae roamed about actively just prior to pupation. The shelters constructed by captive larvae may simulate natural pupation sites not available in the rearing bags such as holes and crevices in twigs or soil or tunnels and gaps in leaf litter. I was unable to find pupae on the host plant in the field, which, together with the increased activity prior to pupation, suggests that pupation in nature occurs either off the host or in concealed niches on the host somewhere other than in the current year's foliage.

The inner surface of the cocoon is lightly lined with silk throughout. Silk is heavier around the seams and at the posterior end where the cremaster is attached.

The Taxonomic Position of *Ellabella*

Because adult characters indicate that *Ellabella* Busck is not in Ethmiidae nor in any other gelechioid family (Powell, 1973), larval and pupal characters of *E. bayensis* were compared only with the copromorphoid and yponomeutoid superfamilies and families using summaries

of characters (Common, 1970; Heppner, in review), descriptions of larvae (Werner, 1958; Yano, 1959; MacKay, 1972), and by examining preserved larvae from the Essig Museum of Entomology, University of California, Berkeley.

There is considerable disagreement between Common and Heppner on many character states. Some of the discrepancies can be explained by the transfer of some yponomeutoid families of Common to other super-families (Heppner, 1977), by differences in taxa included or examined within a family, and by information which became available subsequent to Common's summary. In some instances, however, I could not resolve the source of disagreement, but most may be due to the poor knowledge of the early stages of these taxa which has made family characteristics difficult to define.

Deciding the taxonomic position of *Ellabella* is further complicated by the absence of any exhaustive cladistic analysis of the higher categories of Lepidoptera either with or without consideration of the early stages. For example, Brock (1971) considered Copromorphoidea to be more ancestral than Gelechioidea, while Meyrick (1928) and Heppner (1977) both believe that Copromorphoidea is derived from the Gelechioidea. Thus, outgroup comparisons depend upon whose judgment is accepted. Despite these problems, there is justification for placing *Ellabella* in Copromorphidae, particularly if the transfer of *Lotisma* to Copromorphidae is correct (Heppner, 1978).

Ellabella bayensis exhibits most of the larval and pupal character states common to the Copromorphoidea (*sensu* Heppner, 1977). The larva has a bisetose prothoracic prespiracular group. With few exceptions, this character state occurs only in the Copromorphoidea and Pyraloidea among the Microlepidoptera. Exceptions include *Scardia* (Tineidae) (Hinton, 1956), *Orthotaelia* (Plutellidae) (Werner, 1958), *Rhabdocosma* (Plutellidae) (Heppner, in review), and *Ocnerostoma* (Yponomeutidae) (Werner, 1958).

Although there are pairs of fragile setae on A7 and 8, the pupa of *E. bayensis* lacks true dorsal abdominal spines. Its pupal shell is not protruded upon adult eclosion. Common (1970) asserts that mobile, well-spined pupae are primitive. Among the Microlepidoptera, non-protruded pupae occur throughout the Gelechioidea and Copromorphoidea and in most of the Yponomeutoidea.

These character states indicate that *Ellabella* is in the Copromorphoidea. With the exception of *Scardia*, the more ancestral Tineoidea and the probably more ancestral Gelechioidea have trisetose prothoracic L-groups. The bisetose state of the Copromorphoidea likely is derived by reduction.

The absence of true dorsal spination and the non-protrusion of the pupa at eclosion are more derived than the Tineoidea, but less derived than the

Gelechioidea whose pupae lack spines, have reduced setation and some mobility of abdominal segments, and are not protruded. In general, the pupa of *Ellabella* more consistently fits the concept of some Yponomeutoidea and Copromorphoidea in that pilifers, labial and maxillary palpi, and prothoracic femora are visible.

Few copromorphoid pupae have been described. However, *Commatarcha palaeosoma* Meyrick (Carposinidae) also has some dorsal setae and similar orientations of facial features and thoracic appendages (Yano, 1959). I compared the pupa of *E. bayensis* with that of *Lotisma trigonana* Walsingham, the only other Nearctic copromorphid genus. *Lotisma* and *Ellabella* pupae exhibit the same facial features and thoracic appendages in approximately the same locations. *Lotisma* pupae have some very frail dorsal abdominal setae and the same abdominal segments as *E. bayensis* are moveable. Unlike *Ellabella*, whose pupae are ensheathed in paper towels, plastic, or dried foliage, captive *Lotisma* larvae spin fluffy silken cocoons between overlapping leaves or in similar narrow spaces.

E. bayensis differs from other Copromorphoidea in larval feeding mode. Most known copromorphoid larvae bore or tunnel stems, roots, fruits, or flowers. However, *Lotisma trigonana* larvae often are external feeders of flowers or fruit, at least in later instars, so endophagy is not a constant feature of the Copromorphidae. At least occasionally, *E. bayensis* also feeds upon flowers, and the presence of one of the smallest larvae in a young leaf suggests that early instars mine leaf buds. Even if this character is not consistent with other copromorphoid larvae, the other shared derived characters of *E. bayensis* and the Copromorphoidea substantiate its superfamily placement.

Ellabella seems not to be a bisetose plutellid genus despite having some characteristics of that family. As with some plutellid larvae (e.g. *Eucalantica polita* Walsingham), the circle of crochets on prolegs of *E. bayensis* is biserial in part (Figure 2). This arrangement could be derived from the ancestral state, a single circle of crochets (Common, 1975), by offsetting some crochets in the circle. By contrast, the mesal penellipse of *Lotisma trigonana* presumably follows a different line of derivation in which a portion of the circle of crochets is lost.

E. bayensis and some plutellids (e.g. *Homadaula*) have protruding pupal spiracles. This may represent a derived state, but it occurs inconsistently among families including Epermeniidae and Glyphipterigidae in the Copromorphoidea so may be significant only at the generic level. However, *L. trigonana* also has protruding spiracles with those on A2 and 3 on triangular lobes as on *E. bayensis*.

Because the character states that *Ellabella* shares with some plutellids are not constant among the Plutellidae and because *Ellabella* possesses the derived character states common to most Copromorphoidea (*sensu* Heppner, 1977), the genus should not be placed in the Plutellidae.

Family characters also support the placement of *Ellabella* in Copromorphidae. D1 is absent on segment A9, and positions of most setae are very similar to those of *Lotisma trigonana* (see MacKay, 1972). *Ellabella* differs in having one rather than two pairs of subventral setae on A1, 2, and 7-9, and the spiracle on A8 is not on a tubercale as on *L. trigonana*. The submental setae of *E. bayensis* are located more caudad than those on *L. trigonana*, and the paired flaplike protrusions from the submentum of *Lotisma* are lacking. MacKay (1972) suggested that these submental characters may define the family, but the copromorphid genus *Isonomeutis*, for example, like *Ellabella*, has tuberculate submental setae and lacks protrusions (Heppner, in review). The submental setae of *Ellabella* are borne on a pigmented V-shaped patch which may represent another manner in which these setae are modified among the Copromorphidae.

The other copromorphoid families are inappropriate. *Ellabella* lacks the following characters of Glyphipterigidae, the only other copromorphoid family in which it has been placed: vestigial abdominal prolegs, spiracles on protuberances, and a large anal plate with stout setae. Moreover, D1 is always present on segment A9 in all copromorphoid families other than Copromorphidae in which this character varies.

Although *Ellabella* does not exactly fit the superfamily and family characters of Copromorphidae, this does not exclude it from the family. The taxa within a higher category define the characters of the higher category. Thus, in a poorly surveyed family such as Copromorphidae, the addition or exclusion of any genus may alter the presumed character states of the family considerably. Moreover, the notion that a suite of invariable characters defines the higher category presupposes that no evolutionary intermediacy exists. *Ellabella* may represent an intermediate genus, but its similarities to *Lotisma* and derived character states shared with the Copromorphoidea add validity to its assignment to Copromorphidae.

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A New Subspecies of *Lycaena editha* (Mead) (Lycaenidae) from Nevada

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Abstract. A distinct *Lycaena editha* (Mead) is described from Nevada. It is characterized by its pale aspect and faint maculation. This adds one more to the list of pallid phenotypes from the Great Basin.

The copper *Lycaena editha* (Mead) is locally common in the north-western quarter of the United States and adjacent southern Canada. Two subspecies have been described, the nominate from the western portion of the species' range and *montana* Field from the eastern part. A recently assembled series from the north-central Great Basin of Nevada indicates the existence of a distinct and previously unrecognized phenotype, described herein as:

Lycaena editha nevadensis Austin n. ssp.

Fig. 1, 2

Male (based on holotype and 22 paratypes) **Dorsal Surface.** Ground color Army Brown (capitalized colors after Smithe, 1975, 1981). Primaries with relatively distinct black cell-end bar and less distinct, sometimes absent, subbasal macule. A few specimens with faint basal macule. Secondaries with indistinct, black cell-end bar. Cells Cu1-Cu2 and Cu2-2A and, often, cells anterior to M1-M2 with marginal black macules indistinctly capped or encircled with Flesh Ochre. **Ventral Surface.** Ground color from nearly white to Pale Pinkish Buff. Primaries with prominent, black cell-end bar, black subbasal macule and, usually, small basal macule. Variable (sometimes absent posteriorly) postmedian series of small black macules, a mid-cell macule (sometimes absent in Cu2-2A) and submarginal series of brownish macules. Marginal area brownish. Secondary macules brownish, occasionally not much darker than ground color. Macules variably edged with black and indistinctly encircled with white. Marginal macules indistinct except in Cu1-Cu2 where a distinct black macule encircled with pale brownish orange and capped with black. Those in other cells similar but less distinct, appearing blurred. Entire marginal series indistinctly bordered submarginally with white crescents.

Female (based on allotype and 21 paratypes) **Dorsal Surface.** Ground color as in male to slightly darker Hair Brown. Primaries with prominent cell-end bar, subbasal and, occasionally, indistinct basal cell macules. Cu2-2A usually with dark subbasal macule. Postmedian macules variable from distinct and complete to indistinct and incomplete. Macules in M1-M2 and M2-M3 invariably present. All specimens with, at least, indistinct trace (often prominent and extensive) of orange
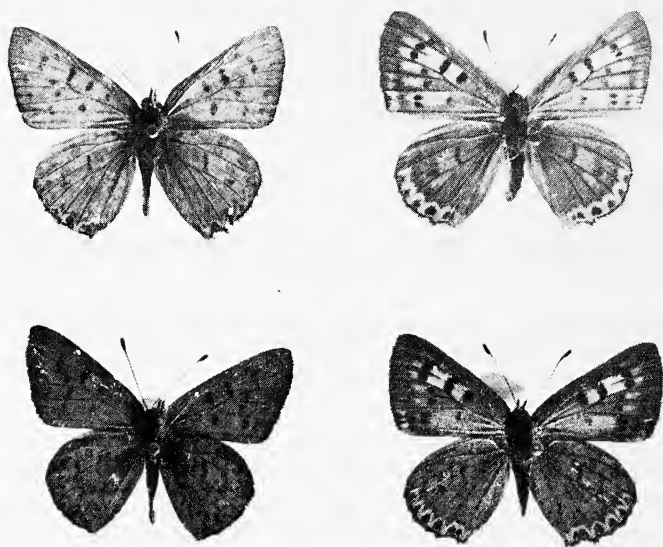
Fig. 1. *Lycaena editha* subspecies. Top, left: *nevadensis* holotype male - NEV:
Elko Co., Jarbidge Mts., Jarbidge Cany., Pine Creek to Gorge Gulch, 30
July 1981, *leg.* G. T. Austin; right: *nevadensis* allotype female - same
data as holotype male. Bottom. left: *editha* male - NEV: Douglas Co.,
Heavenly Valley Ski Area, 6 July 1981, *leg.* G. T. Austin; right: *editha*
female - NEV: Douglas Co., Carson Valley, Scossa Ranch, 3 July 1982,
leg. G. T. Austin.
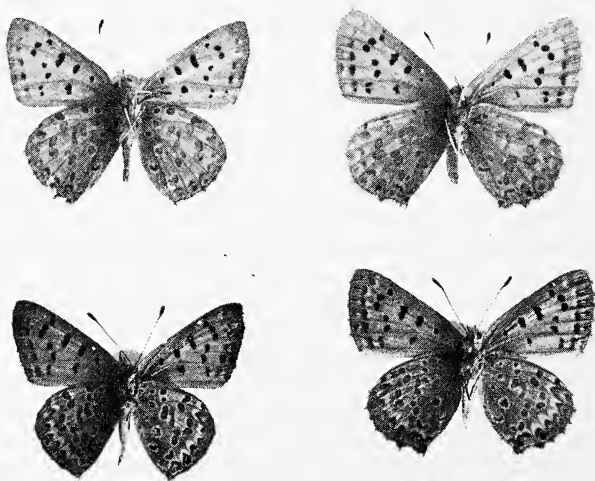
Fig. 2. Same specimens as in Fig. 1.

(color variable including Salmon Color, Warm Buff, Spectrum Orange, Chrome Orange) patches basally in M1-M2 and M2-M3, occasionally involving all cells anterior to vein 2A. Usually relatively distinct irregular marginal orange line (of the same color as orange patches or of brighter orange) from posterior border anteriorly to usually Cu2 (sometimes Cu1). Secondaries with indistinct cell-end bar and indistinct bar or macules in M1-M2 and M2-M3. Occasional specimens slightly paler in M1-M2 and M2-M3. Cells M1-M2 through Cu2-2A with marginal black macules (often double in Cu2-2A) encircled with Chrome Orange (occasionally paler). **Ventral Surface.** Ground color of primaries varied from nearly white to Pale Pinkish Buff to pale Salmon Color. Maculation similar to male but more often complete and distinct. Submarginal macules in Cu1-Cu2 and Cu2-2A often with orange flush distally. Secondaries varied in ground color from nearly white to Pale Pinkish Buff to Drab. Maculation as in male but often less distinct, especially basally. Marginal series more distinct and defined.

Size (length in mm of primary along costa from wing base to greatest extent). Holotype = 16.0, allotype = 15.7, all ♂ types = 15.9 (15.1-18.4, N=21), all ♀ types = 15.5 (14.3-16.5, N=21).

Type Locality. NEVADA: Elko County; Jarbidge Mountains, Jarbidge Canyon between Pine Creek and Gorge Gulch, 6600', T46N, R9E, S33 on USGS Jarbidge, Nev.-Idaho quadrangle, 15 minute series (1943). This area is about 4 km south of the town of Jarbidge on the floor of a narrow, steep-sided canyon.

Types. Holotype ♂: NEVADA: Elko Co.; Jarbidge Mountains, Jarbidge Canyon, Pine Creek to Gorge Gulch, 30 July 1981, *leg.* G. T. Austin. Allotype ♀: same data as holotype. Paratypes (all specimens examined from NEVADA: Elko County; Jarbidge Mountains are considered paratypes, *leg.* G. T. Austin unless specified otherwise, 22♂, 21♀): same data as holotype (11♂, 2♀), Bear Creek, 4.7 mi. S. Jarbidge, 7 Aug. 1980 (2♂), Charleston, 7 Aug. 1980 (2♂, 16♀), 76 Creek, 3.0 mi. N. Charleston, 7 Aug. 1980 (1♀), Jarbidge, 11 July 1971 (1♂, *leg.* P. Herlan), 1 Aug. 1963 (2♂, 1♀, *leg.* P. Herlan), Bear Creek Meadows, 29 July 1976 (1♂, *leg.* P. Herlan), Pine Creek, 10 July 1972 (2♂, *leg.* P. Herlan), Coon Creek, 12 Aug. 1970 (1♂, *leg.* P. Herlan), 3 mi. S. of North Fork, 26 July 1976 (1♀, *leg.* G. Harjes).

Deposition of Type Material. The holotype, allotype and 8 pairs of paratypes will be deposited in the type collection at the Nevada State Museum, Carson City, Nevada. A pair of paratypes will be deposited in the Allyn Museum of Entomology. The remaining paratypes will be retained by the author.

Additional Specimens Examined (all *leg.* G. T. Austin unless indicated otherwise). NEVADA: Elko Co.; Independence Mountains, Jack Creek Road, 1.7 mi. W. Jack Creek Campground, 27 July 1981 (6♂, 14♀), North Fork Road, 5.1 mi. W. Nevada 225, 27 July 1981 (3♂), 3.8 mi. E. North Fork Summit, 27 July 1981 (1♂), Jack Creek, 4.5 mi. E. Nevada 226, 4 July 1980 (1♂), Nevada 11A, 6.7 mi. E. Nevada 226, 28 July 1981 (2♂), Nevada 11A, 1.7 mi. E. Nevada 226, 23 June 1981 (1♀), Nevada 226 at Nevada 11A, 28 July 1981 (1♀), Nevada 11A, 3.2 mi. W. Maggie Summit, 28 July 1981 (2♀), Nevada 226 and Nevada 11A, Jack Creek to Maggie Summit, 10 July 1982 (2♂, *leg.* S. O. Mattoon), Nevada 11A, Bull Run Basin to Columbia Basin, 11 July 1982 (1♂, *leg.* S. O. Mattoon), Nevada 226, Taylor Canyon, 8 mi. NW Nevada 225, 10 July 1982 (2♂, *leg.* S. O. Mattoon), slopes and summit of Porter Peak, 11 July 1982 (1♂, *leg.* S. O. Mattoon), vicinity of Maggie Summit, 20 July 1973 (1♀, *leg.* S. O. Mattoon), Independence Valley, 10 mi. NE

J. Res. Lepid.

Table 1.   Characteristics of *Lycaena editha* and *xanthoides* populations.

Character	nevadensis[1]	montana	editha[2]	editha[3]	xanthoides
Primary length in mm (N, range) ♂♂	15.9 (35,14.0-18.4)	15.3 (27,14-16.5)[4]	15.7 (41,14.7-17.1)	16.4 (16,15.0-17.9)	18.6 (15,16-20)[5]
♀♀	15.7 (39,14.4-16.8)	15.1 (22,14-16)[4]	15.6 (28,14.0-16.7)	16.3 (2,16.3,16.3)	18.7 (15,16.5-20.5)[5]
Spot in M2-M3 ventral secondaries (width in mm, N) ♂♂	1.11 (34)	1.37 (24)[4]	1.06 (41)	1.03 (16)	0.56 (11)[5]
♀♀	1.30 (41)	1.61 (17)[4]	1.25 (28)	1.00 (2)	0.65 (11)[5]
Dorsal ground color	Army Brown	Burnt Umber	Burnt Umber	Burnt Umber	Army Brown
Ventral secondaries ground color ♂♂	Whitish to whitish tan	pale tan	pale tan	pale tan	pale tan
♀♀	pale tan	pale tan	tan	pale tan	pale tan
Ventral maculation primaries	small, some often absent	large, all usually present	large, all usually present	large, all usually present	large, all usually present
secondaries	large, indistinct	very large, prominent	large, prominent	large, prominent	small, prominent
White submarginal band, ventral secondaries	wide, indistinct	wide, indistinct	wide, distinct	wide, distinct	narrow, indistinct
Dorsal secondaries, pale line distal to marginal black spots in ♀♀	usually narrowly present, orangish	indistinct, orangish	indistinct or absent, orangish	indistinct or absent, whitish or orangish	usually prominent, white

[1] all from Elko County, Nevada
[2] all from Douglas County, Nevada
[3] all from 10-16 mi. SW Mt. Shasta, Siskiyou County, California
[4] from Scott (1979)
[5] from Scott (1979, San Diego County population)

Tuscarora, 10 July 1982 (1♂, 1♀, *leg.* S. O. Mattoon), Owyhee River Valley, Wild-
horse Creek Campground, *ca.* 10 mi. S. Mountain City, 8 July 1978 (1♂). Humboldt
Co.; Santa Rosa Mountains, Cabin Creek, 5.1 mi. S. Windy Gap, 13 Aug. 1981 (3♂),
Sheldon Antelope Range, Dufurrena Ranch, 28 July 1980 (1♀).

Geographical Range and Phenology. To date, the new taxon is known only
from north-central Elko County (Jarbidge and Independence mountains) and
northern Humboldt County (Santa Rosa Mountains and Sheldon Antelope Range),
Nevada. Colonies probably exist in, at least, adjacent southwestern Idaho and
southeastern Oregon.

There is apparently one brood with adults present over a one and one-half month
span from 23 June to 13 August.

Etymology. The subspecies is named after the state of Nevada, its only
currently known range.

Diagnosis and Discussion

The discovery of this pallid form of *editha* adds one more to the growing
list of pale phenotypes known from the Great Basin. The first impression
of a series of the new taxon is *editha* which has been exposed to light too
long and are thus faded. The dorsal surface is considerably paler than
nominate *editha* with a narrow terminal line. The ventrum is ghostly white
compared with the richness of color in *editha*. The spots of the primaries of
nevadensis are reduced in size and are often wanting. The maculation of
the secondaries is indistinct, usually not much darker than the ground
color and the spots are often very indistinctly edged with the black and
white that is so prominent in *editha*. The submarginal white band, although
broad, is nearly lost in the ground color, not distinct as in *editha*. The
marginal spots of both wings are much less well defined than in *editha*. The
characters which distinguish *nevadensis* from *editha* also distinguishes it
from *montana*. In size, *nevadensis* is comparable to *editha*, thus larger than
montana. The main distinguishing features of the *editha* subspecis as well
as nominate *xanthoides* (Boisduval) are outlined in Table 1.

Recently, Scott (1979) suggested that *editha* was conspecific with
xanthoides based on allopatry and two known areas with intermediate
populations. I prefer to treat *editha* as a species distinct from *xanthoides*
(Boisduval).

In Nevada, nominate *editha* is distributed mainly in the western portions
in and near the Sierra Nevada (Carson City, Douglas, Storey and Washoe
counties), in the Toiyabe Mountains (Lander County) and the Pine Forest
Mountains (Humboldt County). The latter are dark and richly marked,
unlike the *nevadensis* from the Santa Rosa Mountains to the east. The
Oregon material that I have seen (Crook, Klamath and Lake counties) also
appear as moninate *editha* as does certain California (Eldorado, Mono,
Placer and Tehama counties) material. A series from near Scott's (1979)
"intermediate" population in Siskiyou County, California (10-16 mi. SW
Mt. Shasta, 26-27 June 1959, *leg.* O. E. Sette) is slightly larger than

Sierran nominate *editha* but is similar in color and pattern to the latter.

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Opinion.   Opinion is intended to promote communication be-
tween lepidopterists resulting from the content of speculative
papers. Comments, viewpoints and suggestions on any issues of
lepidopterology may be included. Contributions should be as concise
as possible and may include data. Reference should be limited to
work basic to the topic.

Rebuttal to Murphy and Ehrlich on Common
Names of Butterflies

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Further to Bobs, Tits, etc., I appreciate the opportunity to respond to
Murphy and Ehrlich (1983). When I initiated the Joint Common Names
Committee it was with certain knowledge that it would be a thankless task.
Thus the present response is made in the spirit of patient indulgence of
obvious and inevitable arguments. I am at least thankul that Murphy and
Ehrlich put them forth with a degree of wit and thoughtfulness that
renders them worth reading if not heeding.

It is unfortunate that I was sent their article to rebut rather than to
review. Had I seen it in time, the manuscript might have been rid of a
number of rather egregious errors. These should be dealt with first.
Murphy and Ehrlich claim that "Lack of communication is exemplified by
some of the recently minted 'common names'. . .the 'Mimic,' the 'Elf', the
'Pixie', the 'Laure', and the 'Goldspot Aguna' (Pyle, 1981). Batting poorly,
they attribute all these names to my coinage—while all but the last go back
to Holland or before. Mather (1983) did a little better (.500) in choosing
names said to be of my own invention to criticize—Sunrise Skipper and the
Brigadier were indeed mine, though the Gray Marble and Pale Blue
antedated my field guide. (At least none of these critics went as far as
Shapiro (1975), who labeled my "Bat Blue" (Pyle, 1974) one of the two
worst common names ever, second only to Austin Clark's "Goggle Eye".)
Likewise, Larger Lantana Butterfly (to get back to Murphy and Ehrlich's
dislikes) has precedence with Zimmerman (1958), to distinguish it from
the Smaller Lantana Butterfly—both imported to Hawaii to battle the
weedy Lantana. These authors should line up their ducks better.

Second, Murphy and Ehrlich state that "the Lepidopterists' Society has
recently formed a committee to standardize and presumably stabilize
common names...." The facts are these. After writing the *Audubon Society
Field Guide to North American Butterflies*, for which I was required by the
editors to furnish common names for all species included, I realized

acutely the confusion reigning on this front. Furthermore, correspondence (J. Scott, in litt.) confirmed my suspicion that more and more new common names were on the way in forthcoming books. Therefore I attempted to keep brand new names to a minimum in the field guide, while nonetheless employing rubrics that said more about the organism than simply reiterating the latinized name (e.g., Rockslide vs. Damoetus Checkerspot). In order to bring some order and oversight to this arena, I decided we could do worse than emulate the ornithologists, as we did with the Xerces Society Fourth of July Butterfly Counts (the birders have been through all these things well before us). The American Ornithologists' Union maintains a committee on common names, charged with overseeing changes and standardization of vernacular names for American birds. This committee is accorded almost as much authority as the ICZN has with respect to scientific names.

Therefore, in the summer of 1980, I put first to the Board of Directors of the Xerces Society, then to the Executive Council of the Lepidopterists' Society, a proposal that a joint committee be established. Its remit was to research previously published and proposed English names for North American butterflies, to poll feelings on the matter of preference, and to recommend a list of standard names. Both boards, on which I sat, approved the proposal and, as perpetrator, I was named chairman. Some twenty interested and knowledgeable individuals from both societies have been named to the committee. It has been hoped annually to present the proposed list to the boards for their approval, but the task has not yet been completed.

Now to consider Murphy and Ehrlich's actual arguments briefly. Their first concerns the lack of universality among common names, and the fact that few are really in common use. This is true, and perhaps the term "vernacular name" should be used in preference to the misleading "common name". One goal of the standard list is to increase the general awareness of the preferred names, and their usage.

Second, Murphy and Ehrlich claim that common names do not communicate well, nor do they express relationships. The Nearctic/Palearctic discordance exacerbates this problem. This point is also well taken and well argued in the paper. The ornithologists have had to deal with this, changing the falcon hitherto known as the "Sparrow Hawk" to American Kestrel, since the Sparrow Hawk in Britain is an accipiter, not a falcon; whereas the British refuse to reciprocate by calling their rather pretentious "The Wren" by its North American nomen, Winter Wren.

However, common names do communicate better than binomials to certain people, as I will show below in replying to another of the authors' points. And it is ironic that some common names, such as swallowtail, should remain static and retain far more communicability than the plethora of generic names currently on the books for papilionids. Then too,

everyone is familiar with the story of how the Monarch has borne n scientific names, but has been a Monarch throughout by any other name.

Murphy and Ehrlich interrupt their diatribe to discourse on idiotic names. This is clearly a case of the ear of the beholder. Quite true that chauvinism abounds, and that many common names are misleading. The authors forgot to mention the so-called Lupine Blue, one of the few western plebejines with no lupine association whatever—yet the problem here originates with the scientific name, *Plebejus lupini*! One goal of the Committee is to select appropriate names where available. In any case, one person's idiocy is another's charm or chuckle: the authors must brindle at the colorful common names of English moths (Lesser Lutestring, True Lovers' Knot, Heart and Dart) yet many find them a source of pleasure, and even lepidopterists use them extensively in Great Britain. And as John Hinchliff aptly put it in a letter to me, remarking upon the article in question: "I don't think any serious lepidopterist would expect that a common name would have any scientific value, but we can all use a little romance in our lives." Apparently, Mssrs. Murphy and Ehrlich have no such need.

Finally, Murphy and Ehrlich argue that common names "often have been concocted, mainly at publishers' requests, on the assumption that laypersons cannot learn latinized names." This they find insulting to the public mentality. In this statement they score a hit and a miss. Yes, publishers do request—nay, demand—that common names be supplied for each organism covered in a field guide. There is no way around that for the author, I can aver. However, since field guides will inevitably have common names, is it not better they be standard, so that *Colias nastes* comes out Labrador Sulphur in all texts, instead of that in one, Pale Arctic Clouded Yellow in another, and Nasty Green Sulphur in a third? Such is the case at present. Nor is it an option to suppose that such books will ever rely on latinized names exclusively, for they will not, for reasons Murphy and Ehrlich fail to comprehend. They err subtly but substantially when they suggest that the public is thought not to be *able* to learn Latin names. The unavoidable (and very different) fact is that many nature enthusiasts simply *do not want* to use Latin names, they prefer the vernacular; and that many others are intimidated by scientific names. I have tried to dispell this in all my butterfly books, but it will remain true that Latin scares off some people who might otherwise enjoy the resource, given an easy handle to hang on to. Obviously, any halfway intelligent person *can* learn the binomials. But the insult lies in insisting they should have to do so if they do not wish to.

In their rigorous scientific milieu, which has yielded rich rewards of knowledge, the authors apparently have forgotten how young and uninitiated persons first come into nature's gravitational field. It is not through *Glaucopsyche* and *Shijimiaeoides*. As an author of popular butterfly books

and an experienced teacher of butterfly field classes to children and biologically naive adults, I am certain that English names are a necessary bridge of acquaintance for many persons. Recognizing this, the Ohio Lepidopterists have begun including common as well as scientific names in their newsletter (Eric Metzler, in litt.). It is not important that *Speyeria mormonia* is no more difficult to learn or remember than Mormon Fritillary. What matters is that one is English and one is not. Latin is a roadblock to many a timid mind. It needn't remain that way: those who go on to amateur study quickly begin to learn the Latin, and I always encourage my students to do so as soon as they are comfortable with the idea. But believe me, many intelligent and caring persons would never come to butterflies at all if they did not have common names as cushions to recognition.

And we need those people to care about butterflies. For natural, scarce resources to be protected, they need to have a constituency that cares. This means that many more people than the specialists need to be aware of resources such as butterflies. It is ironic that Murphy and Ehrlich and I should all come down to conservation as the final rationale for our views. They believe we lose time better directed toward saving taxa by worrying about common names, and that to do so is preposterous. I believe that common names serve the conservation of taxa, by making butterflies accessible to people who can make a difference—many, many more people than the serious amateurs and specialists willing to spend time to learn their proper names. Witness the success of the Mission Blue and El Segundo Blue in gathering public support in California, something that *Plebejus (Icaricia) icarioides missionensis* and *Euphilotes battoides allyni* could never do. There would never be room in the headlines, not to mention the value of the romantic appeal lent by the English names.

Murphy and Ehrlich's commitment to conservation is not to be questioned, and I for one know the junior author to be a magnificent teacher of the young—I was one who benefitted from it. However, to insist that common names should be suppressed, that their supposed usefulness is phoney, and that those interested in butterflies should have to learn the Latin, is both doctrinaire and naive. Doctrinaire because it denies a matter of choice that is clearly exercised by the buyers and users of popular guides. Naive, because it ignores the fact that every other branch of natural history is deeply dependent upon vernaculars to appeal to beginners. When wildflowers, trees, mushrooms, mammals, birds, even herps and minerals all have common names (if far from standard in most cases), should we hold out for butterflies, medievally and stubbornly? I say we should embrace them for their limited but appropriate and necessary purposes; and be in the vanguard, right behind ornithology as usual, in standardizing them. The "problem" of common names will not go away, so let us trod on it squarely and turn it from a stumbling block into a stepping

stone.

Murphy and Ehrlich's humor vanishes and they drop from doctrinaire to despotic in their final insistance. Their criticism of Miller and Brown for telling us all what scientific names to use is well known (Ehrlich and Murphy, 1982). So when they insist that "lepidopterists should use latinized names—exclusively!", it seems to me they practice a double standard. If I want to call *Vanessa atalanta* a Red Admiral, I certainly shall; and I suspect most of us would reserve the right to revert to the mother tongue now and again for favorites.

Indeed, in putting forth a list of "standard" common names, it is not the Committee's intention to force anyone to use them. People will call butterflies what they damn well please. The hope for such a list is simply that it will furnish a basis for consistency and help to turn away confusion. At the very least, a valuable historical document should come of it. We should be thankful that our task does not approach that of the ornithologists: the Ruddy Duck alone has owned several dozen colloquial names. Few American butterflies have gathered more than two or three. Further contributions of obscure common names are warmly solicited.

Murphy and Ehrlich call upon the committee to disband itself. They may hope on, but it isn't likely at this point. I would like to thank them for their witty, if too self-serious, vehicle of debate. From this discussion will surely flow a sharper vision of what to call a butterfly in any language. Meanwhile, I have chosen not to reveal some of these authors' own favorite field epithets for elusive checkerspots; suffice it to say that they wildly ignore their own injunction that lepidopterists whould use latinized names exclusively!

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Patronyms in Rhopaloceran Nomenclature

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Abstract. There has been an increasing tendency for many recent authors to assign patronyms to the majority of the new taxa they describe. This practice deviates from the precedent established by Linnaeus, Fabricius, and their colleagues. Nomenclature was originally created to serve as a means of systematic descriptive labelling. Because patronyms fail in this respect, recommendations are proposed which would limit their numbers in future descriptions.

A patronym is a Latinized name of a person assigned to a taxon. People from ancient Greece, such as Hippocrates, Marcellus, and Croesus, have had their names applied to species of Papilionidae. Mythological patronyms abound in our nomenclature and are familiar to all lepidopterists: Eurydice, Diana, Danaus, Atalanta, and Apollo are but a few examples. Feminine names, more so than masculine names, are frequently assigned to new taxa without Latinization. Many actually have Greek or Latin origin and persist unchanged in many cultures. Examples are *anna, annabella, doris, chloe, phoebe, Athena, Patricia,* and *Vanessa.*

This paper does not deal with the above types of patronyms as they were widely used by Linnaeus and his followers and have an appropriate place in modern nomenclature. The purpose of this paper is to call attention to and address the current tendency to give Latinized surnames and Christian or given names to the majority of new taxa. While the surname patronym has been used to some degree since the time of Linnaeus, its present proliferation is cause for concern if the example set by Linnaeus is to continue. A review of names with his authorship (1758) shows he had a great sense of responsibility, a good imagination, and a sensitivity towards assigning descriptive and meaningful names.

Descriptive names are not here advanced as being the only or best alternative to patronyms, but they are one of the more useful alternatives, and this advantage will be discussed. Other useful names can be created from geographical, classical, barbarous and native names, and other sources listed by Jaeger (1955).

The assignment of patronyms is certainly a personal activity, on behalf of both the author of the name and the recipient whose name becomes that of the taxon. Because of this personal nature, and, to state it bluntly, because

many egos are involved, I will not cite authorship of the patronyms used as examples in the following discussions. It is not my intent to unjustly criticize or put on the spot any one author or claim that his contributons to lepidopterology are not valuable: this is not a personal attack. It is also not my intent to judge the worthiness of any patronym recipient. The examples to be cited are meant only as examples of a general trend and are not singled out to embarrass any one person or group of people.

Is there a problem? If the only purpose in assigning labels to entities was to assess the number of entities in the world, then Arabic numerals would suffice: species 1, 2, 3, and so on. But nomenclature exists for descriptive reasons, and patronyms fail in this respect to nearly the same degree as numerals.

It is unfortunate that all who would like to be doing taxonomic revisionary work are not able to do so, but such are the demands of our society and economy. Of those workers fortunate enough to be in such situations are many who have shown a total or strong bias towards assigning patronyms. There are authors who have given identical patronyms to collections of different new species. Others have indiscriminately assigned patronyms to honor every relative, colleague, acquaintance, and friend-of-a-friend, and when it appears they have exhausted their lists of personal names, they start over again by assigning the same patronyms to new taxa. These practices show a total lack of imagination and absence of taxonomic creativity with no regard to the butterflies burdened with their names or other lepidopterists who must use the names. The situation has become the worst with the neotropical Rhopalocera, where most new taxa are found, but is prevalent among more recently described nearctic butterflies.

To illustrate this trend, a review of all the generic, specific, and subspecific names was made using Miller and Brown (1981). The year of original description of each taxon was noted and these were summarized by decade. The percentage of all names that are patronyms was computed. The results are presented in the graphs in Figures 1 and 2. The progressive increase in the number and percentages of patronyms is obvious.

What are the probable reasons taxonomists assign patronyms when so many other appropriate alternatives exist? It would be difficult to pose this question to authors so biased without causing some suspicion, animosity, or implied disapproval towards their work, but from a review of patronyms in use it is not difficult to summarize the main reasons they have been given. Listed in suspected order, the most frequent first, the reasons patronyms are given are:

1. To honor a colleague, collector, or discoverer. This honor has been bestowed upon both great and not so great lepidopterists, as well as biologists from related disciplines. All the notable lepidopterists of the past have been immortalized in the literature: *Fabriciana, Batesia,*
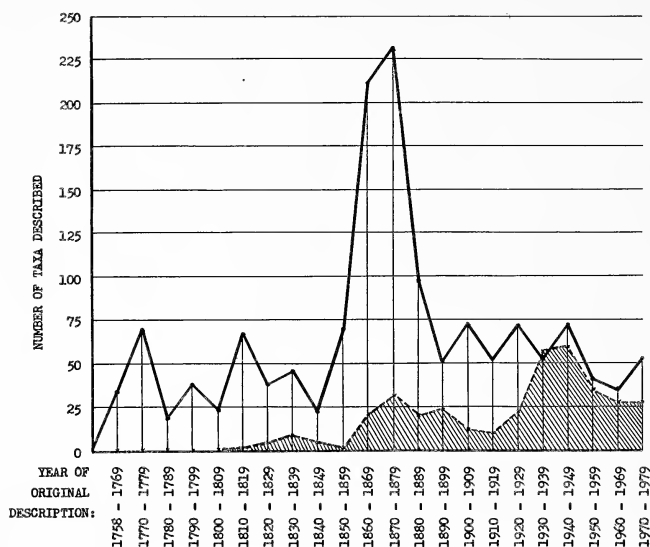
Fig. 1. Numbers of taxa described from 1758 to 1979, summarized by decade. Solid line: nonpatronyms. Dashed line, shaded area: patronyms.
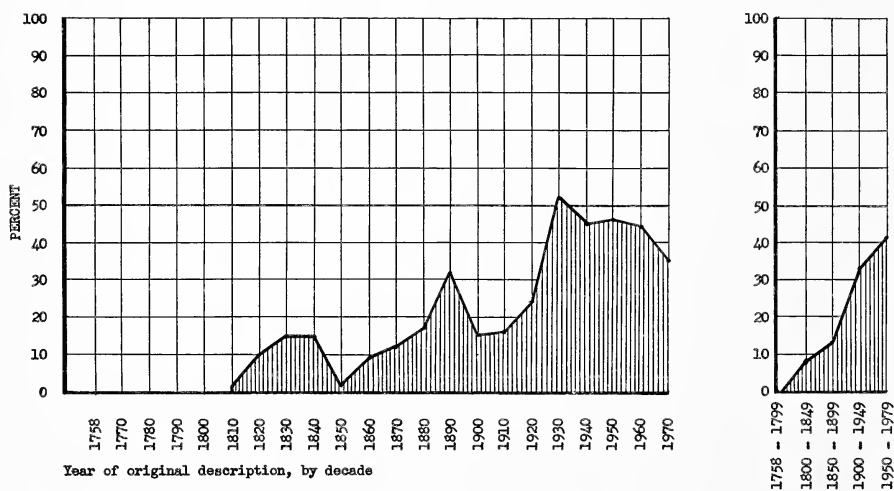

Fig. 2. Percentages of new taxa described as patronyms. Left graph: percentages of patronyms (shaded area) summarized by decade. Right graph: same, summarized by 50-year intervals (except beginning and ending years).

hollandi, comstocki, martini, wrighti, and *edwardsii* are but a few. A greater number of lepidopterists from the present are now receiving their own patronyms, and because many are receiving more patronyms than past notables, the question arises, is a living lepidoperist more notable with, say, four patronyms than a past lepidopterist is with only one? Also, how many times must the same person be honored with patronyms before he is considered adequately honored? As with any award or honor, the more abundantly it is bestowed, the less its prestige. Lepidopterists, as with all biologists, are remembered and regarded more for their work and contributions to science than for the number of patronyms they bestow or receive, and our organizations have created their own appropriate awards for honoring these achievements.

2. To honor a spouse, family member, or relative. Because spouses and family members frequently accompany lepidopterists on collecting expeditions and are inevitably volunteered into some amount of collecting assistance, they are natural recipients for patronyms. In our society male lepidopterists unfortunately vastly outnumber female lepidopterists, so it is the male's spouse that is usually the patronym recipient, and the large number of feminine patronyms in the literature is evidence of this fact. Some feminine given names lend themselves to Latinization more readily than others, as stated in the introduction, and no objection is made to these cases. Andria, Anna, Barbara, Berenice, Helena, Iris, Julia, Laura, Rita, and Stella are all in use in western society and appear in nearctic nomenclature unchanged. The objection is made to those names which must be amended and therefore become obvious patronyms: *jacquelinae, joanae, beulahae, juliae, estelleae, mariae, florenceae,* and *gayleae* are only a few examples.

3. A real, implied, or imagined obligation to a sponsor or employer. The threat of losing one's funding or employment could be, and probably is, a reason that a worker would want to shower his benefactor with patronyms. The situation may be as mild as a desire to show the supervisor what a fine job the worker is doing and how much gratitude he has for his sponsor. At the other extreme, the employer or sponsor may insist that his workers assign patronyms in honor of their superiors, who are unable or unwilling to do the work themselves. Similar relationships may exist between instructor and student or researcher and field collector, however in this last case it is the collector who expects to be honored with patronyms if the researcher wishes to continue receiving the collector's specimens.

4. "It's easier to give a patronym than it is to think up a meaningful, descriptive name." Possibly so, but after all the time spent in research, study, and preparation of the new species and its original description, the few moments it takes to apply a descriptive name to some aspect of the insect which makes it unique, or merely interesting, should be a simple task for a researcher of any integrity. There are even books available to

make this work easier (Borror, 1969; Jaeger, 1955). If the worker is still unable to come up with an appropriate name, he can surely accept suggestions from his colleagues.

5. "I have so many new taxa to describe, I don't have the time to dream up descriptive names." The preceeding comment applies to this statement. Linnaeus, Fabricius, and Bates certainly had no problems coming up with names for their hundreds of new taxa.

6. One-upmanship: "I've got more species named after me than you have." It is hard to believe that in a scientific community such as ours this attitude exists, but in fact it does. The application of patronyms for this reason alone is currently in practice. An appropriate response to this unprofessional, immature attitude eludes me.
immature attitude eludes me.

When a researcher has discovered that the insect before him represents an undescribed taxon, what would be the advantage of assigning a descriptive or other nonpatronymic name to it? A descriptive name would call attention to some difference between it and related species. From its name alone, we know that *Asterocampa subpallida* (Barnes and McDunnough) differs from other *Asterocampa* in having a pale underside. We know somthing of the habits of *Aglais urticae* and *Vanessa cardui* because Linnaeus named them after their larval foodplants. We also know something of the distribution of *Coenonympha california* Westwood, *Thessalia chinatiensis* (Tinkham), *Limenitis archippus floridensis* (Strecker), and *L. astyanax arizonensis* (W. H. Edwards) from only their names, as well as the habitats of *Apodemia mormo deserti* Barnes and McDunnough, *Erebia disa subarctica* McDunnough, and *Callophrys dumetorum* (Boisduval). Even though *Euphydryas editha nubigena* (Behr) is not literally born in the clouds, its habitat, from treeline to 12,000 feet, is frequently enshrouded in clouds. Thus *E. e. nubigena* is doubly blessed with a name that is both descriptive and aesthetic.

Given the nymphalid genus *Polygonia* Hubner, it is a fairly safe assumption that most lepidopterists, even if they had never before seen the following species, would have a good chance of associating the correct name with the correct specimen: *Polygonia* ("many angles") *interrogationis* (Fabricius), "question mark"; *comma* (Harris), "comma"; *g-argenteum* Doubleday and Hewitson, "silver g"; *c-album* (Linnaeus), "letter c"; and *c-aureum* (Linnaeus), "gold c". It is also probable most readers would have a good chance of recalling other members of the genus following a review of their habits and habitats: *satyrus* (W. H. Edwards), from the Greek *Satyros*, a sylvan (forest) diety; *faunus* (W. H. Edwards), from the Latin *Faunus*, a diety of fields and herds; *hylas* (W. H. Edwards), from the Greek *hyle* and Doric *hyla*, a wood: in Edwards' name meaning "belonging to the forest"; *silvius* (W. H. Edwards), from the Latin *silva*, a wood or forest, again in this usage meaning "of the woods"; *zephyrus* (W. H. Edwards),

from the Greek *Zephyros*, the west wind, probably referring to both its flying ability and its western distribution. There are further examples in this genus, but these names are sufficient to illustrate the descriptive and aesthetic possibilities available to all authors. W. H. Edwards certainly demonstrated a professional sensitivity in this genus.

Contrast the preceeding names with the following patronyms. It is unlikely that anyone who has not made a concerted effort to memorize the associations between names and butterflies could take a box of unlabelled specimens and, without references, attach the appropriate names. These names reveal nothing about any aspect of the insect: (Hesperiidae): *Stallingsia jacki, S. smithi, Turnerina hazelae*, and in the genus *Agathymus: judithae, macalpinei, hoffmanni, baueri, freemani, ricei, rindgei, gilberti, micheneri, escalantei*, and so on. Or, for another example, new species of *Calephelis* (Riodinidae), all described in 1971: *C. freemani, dreisbachi, stallingsi, matheri, clenchi, browni, schausi*, and *burgeri*. Or *Cyllopsis* (Satyridae) species: *freemani, windi, dospassosi, henshawi hoffmanii, nabokovi, escalantei, schausi, diazi, steinhauserorum, nelsini, jacquelineae*, and *rogersi*. The only information we can be sure of is that the authors of these names knew, to some degree, the person whose name was patronized.

These contrasting examples illustrate only one of the advantages of descriptive names over patronyms, and no claim is made here that all nonpatronyms will as easily lend themselves to associations. Mythological patronyms may not be directly descriptive, but when the mythology behind the name is known, the application is often clarified. Parnassus is a mountain in Central Greece and in mythology was sacred to Apollo. This relationship was recognized by Linnaeus as similar to the relationship *Parnassius apollo* has with its mountain habitat, hence the name he assigned to the butterfly. Further examples in our nomenclature can easily be investigated with a good dictionary or book on Greek mythology. The creation of descriptive and nonpatronymic names can be so interesting and rewarding it is puzzling that so many authors are biased against them.

What can be done to reverse the trend of assigning patronyms and reestablish nomenclature as a more descriptive system? The following recommendations are hereby proposed as a guide for authors creating new names for taxa. I recommend that:

1. Patronyms be limited to 1 in 20 new taxa. An author must not assign a patronym until after he/she has already described 19 taxa by nonpatronyms.

2. Patronyms not be available for taxa higher than species rank.

3. Double and triple patronyms be unacceptable. (For example: *Erebia youngi rileyi, Limenitis weidemeyerii oberfoelli*; triple patronyms would have the Genus, species, and subspecies all patronyms.)

4. A patronym not be acceptable for use in a genus until after 19 taxa in

that genus receive nonpatronyms.

5. Patronyms not be acceptable for use in an existing genus in which more than 5% (1 in 20) of its species already have patronyms.

6. Any one person not receive more than one patronym, whether from his/her surname or given name.

7. For a family of collectors or biologists, the same surname patronym be used only once.

8. Anagrams of patronyms be unacceptable, including those made from parts of 2 or more personal names. (*Aremfoxia, Harkenclenus*.)

9. Binomial, trinomial, or hyphenated surnames be unacceptable for patronyms, and surnames preceeded by particles be unacceptable. (Examples: *mcalpinei* (sic), *mcfarlandi* (sic), *mcisaaci* (sic), *Mcclungia* (sic): "If the surname begins with the particle *Mac, Mc,* or *M'*, the particle is written *Mac* and combined with the rest of the name." (Borror, 1960))

10. The addition of a Latinized prefix (*pseudo-*, *neo-*, etc.) does not change the fact that the name is still a patronym and therefore is subject to these recommendations. (Examples: *pseudocarpenteri* (sic); *pseudorotgeri* (sic): "Proper names should not be used with other roots in the formulation of scientific names." (Borror, 1960))

11. Geographical place names that are also surnames not be used to circumvent the above recommendations.

Had Linnaeus established the unacceptability of patronyms it is likely we would still be following his example today. However, I am not Linnaeus, and the preceeding recommendations will probably not be taken seriously by most readers and will certainly be instantly dismissed by those now assigning patronyms to the greatest degree. Their arguments are not difficult to predict.

Some authors may argue that we are free society of scientists and to restrict their choices of names is an infringement of their personal freedom. Their freedom is already restricted. The very existence of the International Code of Zoological Nomenclature is testament to the desire of the scientific community to impose order in an area where disorder would otherwise result. Above and beyond any author's "right" to name an insect whatever he wants is his obligation to the entire scientific community. He has a responsibility to all his colleagues to assign an appropriate name to a new insect because this name will forever be in the literature and will be used by others long after he and the patronym honoree have, passed on. A statement by Ehrlich (1957) is still very appropriate: "...a scientific name is a tool, not an end in itself. A person's name after a scientific name is in no way an honor; it is there to fix the *responsibility* for that name on the individual proposing it." (Italics his.) This principle should be posted above every nomenclaturist's desk.

Other authors will argue, "I discovered it. It's my bug and I'll name it whatever I want." There are two important points to be made about this

argument. The first is that butterflies, like all organisms, are public domain and belong to no one person, not even the authors of their names, but to everyone. A patronym implies possession, as does its equivalent common name. *Limenitis lorquini* is commonly called "Lorquin's Admiral", not the nonpossessive "Admiral named after Lorquin". Second, an author does not actually have the right to name an insect whatever he wants, as his choices, as stated previously, are somewhat regulated by the I. C. Z. N.

Patronym recipients may claim, "I have four species names after me. This has encouraged my perseverance in the pursuit of entomology and caused me to think even more highly of the names' authors." The bragging aspect of this remark was discussed above under "One-upmanship". There are no species named after me and my lepidopterological enthusiasm is very intense: the subject becomes more and more interesting every year. No one in our discipline would argue that lepidopterology was not inherently fascinating, but if one's interest is subject to, and is proportional to, the number of patronyms with which he is so honorably showered, then perhaps he is in lepidopterology for the wrong reasons. Would his interests diminish if one or more of his own patronyms was sunk into synonymy? To think that the action of having one's name bestowed upon an animal (or plant) will somehow bring some prestige and recognition to that person is very curious, but this is probably a subject more appropriate for study in *Psychology Today*.

There will likely be other arguments supporting the continued prevalence of patronyms, but they can only be self-serving. In conclusion, I hope this discussion has put light on the patronym problem. As stated by Ehrlich and Murphy (1982), "Taxonomists should not be creating nomenclature primarily for their own use, but as a general tool useful to all biologists." This statement is directly applicable to those assigning patronyms.

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Notes

Notes on Maryland Lepidoptera No. 11: Six New Butterflies for the State of Maryland

We are all familiar with the destruction of our natural habitats caused by "so-called" improvements and modernization. With such habitat destruction, it is increasingly difficult to discover new species and populations in Maryland. However, with persistent field work, one is occasionally rewarded with finding a new population or species.

On May 17, 1953, a field trip was made to Loch Raven Reservoir. At a mud puddle on the east side of the lake, numerous butterflies were sipping moisture from the edge of the puddle, including approximately 30 male *Papilio glaucus glaucus* L. One was an ochreous colored male. When flying, this specimen appeared to have a color similar to *Speyeria cybele* (Fabricius). When shown to our late friend, Frank Chermock, he wanted to know where it had been collected in Florida, since the specimen appeared identical to *Papilio glaucus australis* Maynard. Although it is extremely unlikely that this specimen is *P. g. australis*, it is interesting to note that an "*australis*" color morph does occur in our area.

For many years we have collected *Poanes aaroni aaroni* Skinner in Maryland, most notably in salt marshes at Chesapeake Beach, Calvert Co., MD. It is primarily a resident of the salt marshes of the Coastal Plain. In Maryland the species is bivoltine, occurring in June and August. The June brood usually represents a color and size typical of *P. a. aaroni*. However, in some areas the second brood has a color pattern and large size typical of *P. a. howardi* Skinner.

Frank Chermock believed these specimens had also been collected in Florida, because of their resemblance to *P. a. howardi*. Thus it appears that in Maryland *P. aaroni* is seasonally dimorphic in certain populations, with the gen. II pheno-typically resembling the southern subspecies *howardi*. The presence of these color and size variants indigenous to Maryland is noteworthy, and should be studied further with controlled breeding experiments.

There are several localities in Maryland that are very good for collecting some of the more uncommon butterfly species, such as the Green Ridge Mountain area of Allegany County. At Fifteen Mile Creek, north of the old U.S. Rte. 40, Dr. John Mason on June 6, 1981, took a fresh specimen of *Limenitis arthemis arthemis* (Drury). Bill Grooms later took one specimen of the first brood on June 21, 1981, and two from the second brood on August 5, 1981. At the same locality on June 17, 1982, Andersen, on a field trip with Simmons, collected a fresh specimen.

On the same day Bill Grooms collected the *L. a. arthemis*, he also took several "proserpina" Edwards forms. On June 15, 1982, Phil Kean collected another fresh "proserpina". Grooms, in company with John Fales, collected the extremely rare aberration *Liminitis arthemis* "cerulea" Ehrmann there also on June 23, 1982, while it was puddling. All three of these butterflies constitute new records for Maryland, however, it should be mentioned that "proserpina" and "cerula" are color morphs.

We have suspected that *Satyrium kingi* (Klots & Clench) would be found in Maryland, especially on the Eastern Shore or in southern Maryland. On July 23, 1982, Andersen made a field trip to the Millville area of Worcester County,

Maryland, on the southern end of Maryland's Eastern Shore. He selected this area because he had seen much sweet gum, *Liquidambar styraciflua* (L.), growing here in the spring of the year, which has been associated with the ecology of *Satyrium kingi*. While walking down a sandy road in a wooded area, he noticed a hairstreak fly across the road in front of him and land on a gum leaf. As he carefully approached the butterfly, it became wary and slowly flew deeper into the gum tree and surrounding bush. On probing, the butterfly did fly out and landed on a white cedar leaf, *Chamaecyparis* thyoides, across the road. After netting and examing the specimen, it proved to be a female *Satyrium kingi*, a first for Maryland.

The six new records for the State of Maryland may be summarized as follows: Variations/aberrations—

1. *Papilio glaucus* "australis", morph, May 17, 1953, near Loch Raven Reservoir, Baltimore Co., MD.

2. *Poanes aaroni* "howardi", morph, September, 1953, Chesapeake Beach, Calvert Co., MD.

3. *Limenitis arthemis* "proserpina", June 6, 1981, Fifteen Mile Creek, north of the old U.S. Rte. 40, Green Ridge Mountain, Allegany Co., MD.

4. *Limenitis arthemis* "cerulea", aberration, June 23, 1982, Fifteen Mile Creek, north of the old U.S. Rte. 40, Green Ridge Mountain, Allegany Co., MD.

New species for Maryland—

5. *Limenitis arthemis arthemis*, June 6, 1981, Fifteen Mile Creek, north of the old U.S. Rte. 40, Green Ridge Mountain, Allegany Co., MD.

6. *Satyrium kingi*, July 23, 1982, near Millville, Worcester Co., MD.

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Incidence of the Black-backed Larval Mutant of *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae) in Ukrainian SSR

Evidence of the presence of black-backed larval mutants of *Lymantria dispar* in Japan was reported by Schaefer and Furuta (J. Res. Lep. 18:167-170). As that report went to press, Schaefer had another opportunity to observe black-backed mutant larvae of *L. dispar* in material which was collected in the Ukrainian SSR, USSR. Based on this material, we provide further insight into the incidence and distribution of the black-backed mutation in Asia.

Larvae were collected 1-7 June 1981 by the junior authors and others in the touring party, at four locations in the Ukrainian SSR (Table 1). Collections were made at random and included all available larvae, which were then transported to the quarantine facility at the Beneficial Insects Research Laboratory, USDA, Newark, Delaware, to recover any parasites (none of which are recorded here).

Details on the collected material and incidence of black-backed mutants are tabulated in Table 1. Twenty-two black-backed mutants (1.79%) were observed in the sampled population (1228). This included 8.00% mutants of 100 larvae and 3.34% mutants of 299 larvae at Zaporozje and Kherson, respectively. The larval characters of the mutants were similar to those observed previously in Japan (see Schaefer & Furuta Ibid). Three male and 11 female mutant larvae developed into adults while eight died prior to pupation. No obvious character or aberration was

expressed in any of these adults. This was the first opportunity to observe adults which knowingly developed from mutant larvae.

This observation further extends the known range of this mutation within the distribution of *L. dispar*. Documented reports now indicate that the mutation occurs in Japan, Korea, USSR (at least the Ukraine) and Europe (several locations) (sources cited previously), which further supports the belief that this mutation occurs throughout the Palearctic region.

Table 1. Incidence of Black-backed larval mutants of *Lymantria dispar* (L.) from Ukrainian SSR, USSR, as based on field collected material received at Beneficial Insects Research Laboratory, USDA, Newark, DE, in June 1981.

Collection Location	Date(s)	Number Larvae	Number Mutants	Mutants (%)	Host Plant(s)
Mukacevo 48.3° N, 22.5° E	June 5	514	1	0.19	*Quercus* spp., *Fagus* spp. *Populus nigra pyramid-alis* Rozan
Novomoskovsk 48.3° N, 35.1° E	June 1 & 7	315	3	0.95	*Quercus robur* L., *Malus* spp.
Zaporozje 47.5° N, 35.1° E	June 7	100	8	8.00	*Malus* spp.
Kherson 47.4° N, 32.4° E	June 3 & 6	299	10	3.34	*Salix* spp., *Populus nigra pyramidalis* Rozan
Totals		1228	22	1.79	

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Lateral Perching in *Brephidium exilis* (Boisduval) (Lycaenidae) in Texas

Lateral basking and lateral perching has been observed in a number of butterfly species, especially pierids, which appear to use lateral postures in thermoregulation. Satyrids seem to reduce their shadows and maximize cryptic coloration by leaning against the ground. In other families lateral perching behavior is less often reported. It was therefore surprising to find a striking example of it in the Pigmy Blue, *Brephidium exilis*. The purpose of such behavior in this species has not been studied, but may well be protection against mechanical damage from wind. Shields (1974, Jr. Lep. Soc. 28:78) reported a similar phenomenon in *Euphilotes rita* in a sandstorm.

On 13 December 1981, on the shore of Nueces Bay, near Portland, San Patricio Co., Texas, my wife Kay reported seeing a number of specimens of *B. exilis* perched on the terminal shoots of an *Atriplex* species (Chenopodiaceae) and other non-chenopod marsh plants, holding their wings horizontally and folded tightly together. Since the day was overcast, steady at 16°C, and with an estimated 14-20 knot wind, as reported by the U.S. Weather Service and verified locally with a hand-held anemometer, I was quick to note and photograph the occurrence. Within a short period of observation (between 1330 and 1445 CST) at least 45 specimens were observed. They were generally aggregate in distribution, six or eight often being seen within a few meters. All were within 30 to 60 cm above the ground, clinging to the tops of the thin, stemmy vegetation, and all were positioned within about 25 degrees of horizontal (Fig. 1). Their various slight tilts were not accurately aligned with the sun, which was totally obscured by clouds. In all cases the wings pointed downwind, as a horizontal flag would fly. In sheltered areas where eddying currents ran counter to the predominant wind direction, it was possible to roughly predict the breeze by observing the compass heading of the wings.
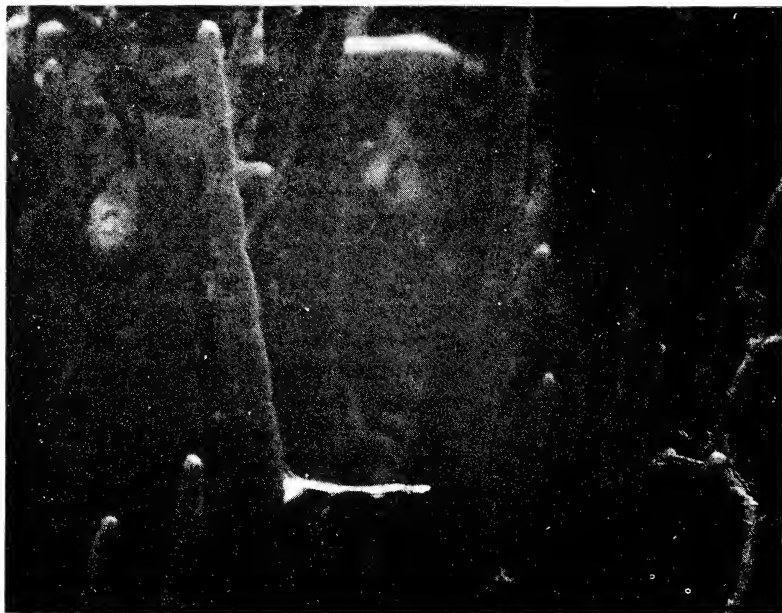
Suspecting that vertically perched specimens might be overlooked, I spent considerable time viewing through the vegetation at eye level, but was unable to find one vertically perched individual.

In all cases the wings were tightly closed, the primaries tucked behind the secondaries. The antennae were always neatly together and projecting forward, fully exposed. All specimens but one were "asleep", reacting very little to being touched, often pivoting slightly on their perches and usually reorienting to a more nearly vertical posture. When picked up and released they appeared unable to sustain flight, fluttering weakly into the deeper weeds without attempting a return

to the previous positions. In some cases the antennae could be stroked with no effect.

At the onset of these observations one specimen was seen flying and alighting twice to bask in the more usual fashion, opening its wings partially and attempting to orient to sunlight, which it could not find. This specimen was seen to pivot 360 degrees before flying out of sight downwind.

The lateral posture of *Brephidium* under these circumstances did not strongly suggest basking or thermoregulating, due to minimization of the exposed wing area. The background vegetation was flecked with disused spider webs which apparently had contained egg cases. At a distance of several meters the similarity of the butterflies to these objects was striking, and it is possible that arthropod or avian predators could be deceived by this "mimicry." Up close, however, these web "models" are quite different in shape and detail from their butterfly "mimics."

While blues in a lateral position are highly visible from above, they are very difficult to see edge-on. Shorebirds or other would-be predators of similar height may have difficulty spotting them. Also, pale colors against a bright, cloudy sky may blend the way fish and other creatures with pale bellies do, as protection from below.

Since this observation was made, on 14 April 1982, at 1320 hours in Barton Creek near Austin, Travis Co., Texas, a single individual of *Echinargus isola* (Reakirt) was seen perching in an identical manner on the petals of a blooming garden *Coreopsis* (Compositae) flower. It was not feeding, and when picked up with fingers and released it was able to sustain flight. The day was heavily overcast and rain was only minutes from falling, but the wind was slight and the temperature nearly 20°C.

I intend to make further observations on this matter and encourage other students to document similar observations and make them available in order to gain an understanding of the phenomenon and its causes.

The author wishes to thank Christopher J. Durden for encouragement in preparation of this note.

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Dione moneta poeyii Butler [1873] in New Mexico (Lepidoptera: Nymphalidae)

The first reported capture in New Mexico of the neotropical butterfly *Dione moneta poeyii* was made on 28 April 1981 at Sunspot (Otero County). The female specimen was taken by hand while nectaring on a yellow composite. Sunspot is located on Sacramento Peak, 9250′ (2819 m) and has abundant, roadside wildflowers present there in the late spring and summer. It is situated in south central New Mexico in the Sacramento Mountains, and offers a montane, conifer woodland habitat characterized by Douglas fir, juniper, Gambel oak, and aspen. The habitat at Sunspot is unlike that at *D. moneta poeyii*'s nearest reported capture site in southwest Texas. Whether this individual specimen is a 'straggler' by Gilbert's (J. Lepid. Soc. 23(3):177-185, 1969) definition or evidence of a local population is impossible to say from a single specimen. Possibly the unusually hot, dry, southerly winds that year played a role in its presence in New Mexico. The specimen was in fairly good condition, but for a pair of beak marks on the hind

Fig. 1. Dorsal view of *Dione moneta poeyii* Butler captured in Otero County, New Mexico on 28 April 1981. Photo taken by R. Faller.

wings. Dr. R. W. Spellenberg (pers. conver.) reported to me that its food plant, *Passiflora*, does not occur in the Sacramento Mountains.

I am indebted to Chris Durden (Texas State Museum) for his search of Southwestern literature and records for references to *D. moneta poeyii*; to Cecilia Miranda who found the specimen; to R. W. Spellenberg (NMSU) for going through his records for *Passiflora*, and to Greg Forbes, Rick Rochette, and Dr. Zimmerman (Entomology Department, NMSU) for their good advice.

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Book Reviews

A Complete Guide to British Butterflies.
Brooks, M. & C. Knight, 1982. 159 pp., ca. 500 color figures; Jonathan Cape, London. Price: £10.95, hardback.

The book is aimed at a wide spectrum of readers making natural history their hobby as well as those taking particular interest in the butterflies and their biology. Every British species is figured in color showing the complete life history from egg to adult, except for a few rare migrants which have not been bred. All figures are color photographs by M. Brooks, some taken in nature, others in captivity. Their technical quality is mostly good, and so is the printing. Nonetheless, the simple technical means available could not produce the quality comparable to pictures produced by such an acknowledged artist as F. W. Frohawk whose work probably served as the model for this book. It must be appreciated that a microscope is not particularly suitable for the photography of eggs and first stage larvae (the loss of structure owing to poor resolution and very shallow depth of field is unavoidable); the "key-hole image" of the pictures is a little disturbing and is perfectly avoidable. Of the photos of adults those of set specimens (some are poorly set, worn and certainly should have been rejected by the authors themselves in the first place) on background of twigs and leaves surely do not look any more natural than if taken on a neutral background. The concentric circles used to show the phenology of each species are not sufficiently clear to give information at first glance, the use of linear graphics would have been much better. The text certainly gives first hand information on every species bred (egg, larva, pupa, butterfly), although it is not necessarily new or better, and more comprehensive than data known from other books. The habitats and distribution in Great Britain are also very briefly mentioned, as well as the external features of adults and the host plants. The introductory chapter is quite comprehensive for this type of book and the topics dealt with include identification, anatomy, variation, enemies and diseases, dispersal, classification, breeding, collecting and photography. The book surely cannot replace Frohawk's book, now out of print, and difficult to come by. It can give a lot of pleasure to read and look at, and it certainly has not been written with commercial success in mind, which is a rare tribute to a more or less popular book on butterflies to appear in the last decade.

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The Mitchell Beazley Pocket Guide to Butterflies.
Whalley, P., 1981. 168 pp., over 900 color figures by R. Lewington. Mitchell Beazley Publishers, London. Price: £3.95, hardback.

Mitchell Beazley pocket guides are slim, narrow books (ca. 9 x 19 cm) on an assortment of topics such as antiques, cheese or wild flowers, to name just three. With the recent inflation of books on butterflies it is hardly surprising to find them included in this series; also the name of the compiler, P. Whalley, who has become doubtless the most prolific contemporary writer about butterflies, fits well with the

whole picture. The book deals with abour 400 species of European butterflies and skippers inhabiting the area west of U.S.S.R. and does not include species from N. Africa; at the end there are some 15 species of common day-flying moths the inclusion of which serves no useful purpose and contradicts the title of the book, and may confuse the less experienced reader at whom this book is clearly aimed. The text consists of eight pages of brief introduction and explanation of numerous symbols used freely throughout the book; stray notes on identification, distribution, flight period, some host plants and other aspects are given species by species, being as brief as restricted space allowed, based chiefly on the well known guide to butterflies by Higgins & Riley. All of this would hardly justify writing a review of the publication in a scientific journal. The over 900 colour illustrations by Richard Lewington contradict completely impressions gained by reading the test: they belong among the best figures of butterflies I have ever seen and are by far the best in contemporary terms. Nearly all species recognized by Higgins & Riley (cf. above) are illustrated, some both upperside and underside for both sexes, and a few caterpillars are added for good measure. The figures are so accurate that it is possible to see which specimens selected for illustration were old and somewhat faded; this is not too bad as the note concerns just a few satyrids. I wonder if *Colias nastes* and *C. myrmidone* have been correctly identified and come from Europe. It is, however, a great pity that R. Lewington left out some species: their inclusion, as well as adequate illustrations of the undersides and both sexes would have made the little book comprehensive. The nomenclature follows Higgins & Riley, with all the useless hair-splitting to increase the number of genus-group names beyond comprehension; names of authors are not given. The exceptional quality of the illustrations makes the book attractive to lepidopterists.

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The Butterflies of Northern Europe.
Björn Dal, 1982. (Translated by R. Littlewood, English edition edited by M. Morris). 128 pp., with numerous unnumbered color figures. Croom Helm Ltd., London. Price: £5.95, hardback.

This slim book of just a little over pocket size is aimed at the layman and deals with a generous selection of butterflies from Fennoscandia (Finland, Sweden, Norway, Denmark) and Great Britain. The introductory chapters give a brief account of the classification, external features and the environment of the butterflies as well as a few lines to encourage their watching (rather than collecting) and conservation. The species are arranged in ecological groups according to the major habitat types, instead of the usual systematic units, which are (1) Bogs and mosses, (2) Woods, parks and scrub, (3) Mountainous and stony ground, (4) Arid grassland, (5) Meadowland and marshes, (6) Cultivated land; although these ecological units are very broad, the classification of some species may be frowned upon as inaccurate. Both English and Latin names are given and each species is provided with a distribution map which is far too small to convey much basic information. The short text which goes with every species may be found attractive by the beginner, but is too brief to be subjected to and judged by the somewhat higher standards of information and accuracy usually expected by more advanced students of the

butterflies. The central point of the book is the numerous (almost on every page) illustraions (water colors) which depict the selected species in all sorts of natural positions including flight, usually on a background of their habitats; they are very pretty to look at but offer only on some occasions details important for identification of the species, the stress being placed rather on their artistic value than their scientific accuracy. The book is well produced and gives an inviting, refreshing impression. It is certain to make a nice present to anyone making the first steps of interest in the butterflies and their conservation, or to help to kindle them among some of those not yet aware of them. Nonetheless, the addition of a few more well written pages of introduction would have done more towards the understanding of the complex relationship between the butterflies and their environment.

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An Introduction to the Moths of South East Asia.
Barlow, H. S., 1982. Malayan Nature Soc., Kuala Lumpur, ix + 305 pages, 50 color plates. Available from E. W. Classey Ltd. Price: £37.50

Some aspects of this book exceeded my expectations, while others were disappointing. The hard cover, binding, printing, etc. appear to be of good quality. The drawings of genitalia are very fine, and one could not wish for better color plates. The text is relatively free of misspellings and typographical errors. German names are missing umlauts and some French names lack accents. The map on the inside front cover has Bhutan mislabelled as Sikkim, and the Moluccas in eastern Indonesia are incorrectly indicated. The number of species treated and figured is lower than I had expected for a tropical region. The four pages devoted to host plant listings seem worthless due to the content and arrangement. Barlow has succeeded in covering fairly well a wide range of topics including morphology of the adult, 'the species concept', phylogeny and classification of the order Lepidoptera, collecting, conservation, and pest species and their control. Discussions under a few of these sections are sketchy, but the title of the book does include the word "introduction," and adequate literature citations in all sections will direct readers toward more detail in other works. The bibliography is rich in literature published in southeastern Asia. Valuable information, new to me, is presented on attraction of moths to light and pheromones. Barlow did well to recognize that certain taxonomic work is best left to trained professional taxonomists: Dr. Jeremy Holloway has therefore provided a 79-page appendix of taxonomic notes.

Since the Saturniidae are my area of specialty, I'll offer a few remarks on Barlow's coverage of this family. Most genera occurring in southeastern Asia are not mentioned. *Actias maenas* cannot reasonably be assigned to the Ethiopian genus *Argema*. Sulawesi is not part of the distribution of *A. maenas* (it is replaced there by *A. isis*). The validity of the name *Samia borneensis* is too uncertain to be used, pending a revision of the genus *Samia*. I would predict that *borneensis* will probably eventually be synonymized under *S. insularis*. Color figures of *Loepantheraea rosieri*, some *Antheraea*, and the female of '*Syntherata*' *loepoides* are especially welcome, the first ones published in some cases.

Economic entomologists dealing with pest species of Lepidoptera will benefit from several chapters. Serious collectors (including those living outside of south-

eastern Asia) having scientific interests in lepidopterology will find the book even more instructive. Taxonomists seeking new information on their particular groups, and/or Indo-Australian zoogeography as it pertains to moths, are more likely to be disappointed. The high price will therefore be justified by some prospective buyers but not by others.

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Blue Butterflies of the Lycaenopsis-Group.
Eliot, J. N. & A. Kawazoe. British Museum (Natural History), London. 1983. 309 pp. 6 color plates, 560 figures. (Available from Rudolph Wm. Sabbot, North American agent for BM(NH), 5239 Tendilla Avenue, Woodland Hills, CA 91364). Price: $63.00.

At last an exception to the faunal fad with its current spate of "The Butterflies of. . ." books. This work should cause all lepidopterists concerned with systematics to reflect, as it is a remarkable able effort by two (very advanced) amateurs, an ex-Royal Artillery officer and a schoolmaster. The extraordinary effort of the former author in his *Higher Classification of the Lycaenidae,* not to mention revising Corbet and Pendlebury, and the latter's senior authorship of *Coloured Illustrations of the Butterflies of Japan,* should provide inspiration and models of what can be done with relatively few simple tools and an active, inquiring, informed brain.

By introduction, an historic background with their system of identifying and selecting types is given. Following a complete checklist we are given a basis of classification. Herein is a brief, but relevant section on balance. The authors stress that generic distinctions in the *Lycaenopsis*-group are clear in contrast to the status of genera in the *Polyommatus* section, wherein by comparable criteria many genera would fall into *Plebejus.*

A discussion of characters and their states follow. The male genitalia are stressed, and a detailed morphology and nomenclature given, including the combination of three unique characters which set the *Lycaenopsis* section apart from other Polyommatinae. Female genitalia, scales pattern and other characters are evaluated. The last of the introductory remarks are two pages on geographic variation and speciation.

Following keys based on genitalia and external characters we have 272 pages of detailed description with genitalia of all 112 species figured by excellent, diagnostic line drawings. All new and previously non-illustrated species are shown, including 6 color plates and a total of 560 figures. Twenty-one genera are considered of which 8 are new. The appendix concludes with a dissertation of the correct use of the name *Lavendularis* Moore 1887. Fundamentally a dry subject, this is actually a superb renditon of a not uncommon procedure which heroically awaits those who wish to clarify nomenclature rather than further clutter same.

By way of criticism, the weakest points are a complete absence of distribution maps, lack of a tabular presentation of phenetic data from which others could reconstruct patterns of relationship, and absence of a hypothesis of phylogeny. From the standpoint of significance to general biology, the first two are the most wanting. Since phylogenetic schemes are usually more fun than fact, the issue is not critical except to provide flavor. Reading the text shows that distributions of the

various genera and species, found chiefly through the Oriental and Indo-Australian regions, have a fascinating pattern of ranges, disjunctions, and geographic limits. Graphic presentation of these data would have greatly strengthened the work.

Deliver us more investigations to attack the morass of Lepidoptera systematics with the skill and dedication of Eliot and Kawazoe—and give these investigators the cooperation of museums and collectors to do the job.

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Population Biology of Tropical Insects.
Young, Allen M., 1982. 526 pp. Plenum Publishing Co., New York. Price: $57.50 ($69 outside U.S. and Canada).

What an infuriating book! It does a job that needed to be done, and it is better than no book at all, but how much better it *might* have been! Its faults are predictable to those who know Young's work. He has done more base-line natural history on Neotropical butterflies (and cicadas, and some other things) than anybody since Bates, and his voluminous personal bibliography attests to that—and it is perhaps understandable that his own papers are so prominently showcased in this review volume. But he has an apparently irresistible tendency to find some trendy theoretical notion to match every observation he makes, and his *ex post facto* ruminations tend to take up much more space in his papers than do the observations themselves. The book is the same way; most of the models advanced by anybody, for anything, in theoretical ecology are presented and illustrated with more or less tenuous Neotropical examples (or, occasionally, with no examples, if Young can't think of one). Perhaps the book ought to have been called "A Relatively Uncritical Review of Theoretical Ecology as Illustrated by Neotropical Insects."

The book does serve a valuable function in pulling together the bewilderingly scattered Neotropical literature, but how effectively does it do so? That is hard to tell, because rather than the conventional alphabetical bibliography, it numbers the text citations and lists them at the end in numerical order. This is one of the least useful kinds of bibliography, even if (as in this case) the authors' names are in the Index with page references to their citations. This is presumably the publishers', not the author's, fault, but it detracts from the book's usefulness in any case.

Make no mistake: so little is known about the population biology of tropical insects that the sheer bulk of this volume advertises how padded it is. It is still worth having if you can afford it (or use it as a tax write-off), but if you can't, the sensible thing to do is to photocopy the bibliography, snip and paste, and transform it into a card file. There are 794 citations on 34 pages. Your card file will then cost you under $10 if you do all the work yourself.

Arthur M. Shapiro, Dept. of Zoology, University of California, Davis, CA 95616

INSTRUCTIONS TO AUTHORS

Manuscript Format: Two copies *must* be submitted (xeroxed or carbon papered), double-spaced, typed, on 8½ x 11 inch paper with wide margins. Number all pages consecutively and put author's name at top right corner of each page. If your typewriter does not have italic type, underline all words where italics are intended. Footnotes, although discouraged, must be typed on a separate sheet. Do not hyphenate words at the right margin. All **measurements** must be metric, with the exception of altitudes and distances which should include metric equivalents in parenthesis. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as example: 4. IV. 1979 (day-arabic numberal; month-Roman numeral; year-arabic numeral). Numerals must be used before measurements (5mm) or otherwise up to number ten e.g. (nine butterflies, 12 moths).

Title Page: All papers must have the title , author's name, author's address, and any titular reference and institutional approval reference, all on a separate title page. A **family citation must** be given in parenthesis (Lepidoptera: Hesperiidae) for referencing.

Abstracts and Short Papers: All papers exceeding two typed pages must be accompanied by an abstract of no more than 300 words. An additional summary is not required.

Name Citations and Systematic Works: The first mention of any organism should include the full scientific name with author (not abbreviated) and year of description. New descriptions should conform to the format: male: female, type data, diagnosis, distribution, discussion. There **must** be conformity to the current International Code of Zoological Nomenclature. We strongly urge deposition of types in major museums, all type depositions must be cited.

References: All citations in the text must be alphabetically listed under Literature Cited in the format given in recent issues. Abbrevations must conform to the *World List of Scientific Periodicals.* Do not underline periodicals. If four or less references are cited, please cite in body of text not in Literature Cited.

Tables: Tables should be minimized. Where used, they should be formulated to a size which will reduce to 4 x 6½ inches. Each table should be prepared as a line drawing or typed with heading and explanation on top and footnotes below. Number with Arabic numerals. Both horizontal and vertical rules may be indicated. Complex tables may be reproduced from typescript.

Illustrations: Color must be submitted as a transparency (i.e., slide) ONLY, the quality of which is critical. On request, the editor will supply separate detailed instructions for making the most suitable photographic ilustrations. Black and white photographs should be submitted on glossy paper, and, as with line drawings, must be mounted on stiff white cardboard. Authors **must** plan on illustrations for reduction to the 4 x 6½" page. Allowance should be made for legends beneath, unless many consecutive pages are used. Drawings should be in India ink at least twice the final size. Include a metric scale or calculate and state the actual magnification of each illustration as printed. Each figure should be cited and explained as such. The term "plate" should not be used. Each illustration should be identified as to author and title on the back, and should indicate whether the illustration be returned.

Legends should be separately typed on pages entitled "Explanation of Figures". Number legends consecutively with separate paragraph for each page of illustrations. Do not attach to illustrations. Retain original illustrations until paper finally accepted.

Review: All papers will be read by the editor(s) & submitted for formal review to two referees. Authors are welcome to suggest reviewers, and if received, submit name & comments of reviewers.

THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

IN THIS ISSUE

COVER ILLUSTRATION: Head morphology (profile) of *Ellabella editha* Busck. See J. B. Heppner article, page 50.

THE JOURNAL OF RESEARCH
ON THE LEPIDOPTERA

Invited Paper

Colias alexandra: A Model for the Study of Natural Populations of Butterflies

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Abstract. Life tables constructed for a natural population of the Pierid butterfly *Colias alexandra*, analyzed key-factor techniques (for 1975-1979), show factors contributing to reduced natality determine the year to year population trends; these are largely density independent factors. These conclusions are consistent with the findings of similar studies and have been corroborated by two subsequent incidental events. The loss of an unusually large number of adult females in 1978 resulted in a population depression in the following year, which was continued for the next two years (e.g. from >.8 to <.4 eggs/sq m). In 1981, an outbreak of the predaceous free-running mite *Balaustium* sp. resulted in a 200% increase in egg mortality (approximately 30% to 60% of all eggs) without a subsequent overall decline in the population's adult (i.e. egg-laying individuals) numbers. The methods and findings of this and the limited number of comparable studies, which examine all life stages and span several years, produce a wealth of information about the individual system and provide a means of verifying the general theories of population ecology.

Introduction

Comprehensive observations of natural populations are necessary prerequisites for the verification of general theories of population ecology and for their subsequent application in management and conservation. Ideally observations should extend over a prolonged period and examine as many environmental factors (biotic and abiotic) as possible. Insects have proven to be useful subjects for the study of natural populations. It is surprising to find, however, as Gilbert and Singer state in their 1975 review of butterfly ecology, that relatively few contributions to insect ecology have come from butterfly research; that picture has only just begun to change (see Dempster, 1983; Strong, 1984). Butterflies, among the most visible of insects, have been important tools for testing and development of evolutionary theory (e.g. mimicry and polymorphism), yet there is a paucity of data regarding factors that limit or regulate butterfly populations. The more extensive studies of butterfly populations

have focused on adults (e.g. Ehrlich, 1965; Ehrlich and Gilbert, 1973; Brussard and Ehrlich, 1970; Brussard et al., 1974; Gilbert and Singer, 1973; Watt et al., 1977, 1979). These studies seriously neglect or ignore the wide range of selection forces that shape the remainder of the complex life cycle of these holometabolous insects. Adult population studies have not provided us with a general understanding of population regulation.

Critical to the complete understanding of the dynamics of a population is the assessment of its demographic attributes, such as the probability of survivorship at a given time or age class. These attributes reflect the adaptations of the population, such as the ability to procure resources, survive climatic extremes, and avoid predators. Notably few life tables, detailing reproduction and survivorship, have been constructed for butterflies (e.g., *Pieris rapae*, Richard, 1940; Harcourt, 1966; and Dempster, 1967; *Lycaena dispar*, Duffey, 1968; *Anthocharis cardamines*, Courtney and Duggan, 1983), although such demographic models have been applied to numerous other insect species. Insight into the causes of population fluctuations can be obtained when life tables can be coupled with an understanding of predation, parasitism, climate and other conditions that affect population numbers.

In the course of several papers, I have presented the findings to date of a continuing long-term study of a natural population of the sulfur butterfly *Colias alexandra* Edwards (Pieridae). I have been concerned with the identification of the demographic attributes of this population and the environmental factors which influence it (Hayes, 1981a & b, 1984), examining specific components of its life history (Hayes, 1982). The results of the study, which was initiated in 1975, represent a nearly unique set of data with regard to the investigation of butterfly population dynamics (see Singer and Gilbert, 1975; Dempster, 1983).

I have addressed two questions basic to understanding the dynamics of a population: 1) what causes fluctuations in the numbers of a species from year to year; and 2) what determines the magnitude of these fluctuations. On the basis of data obtained to date from this study, it is possible to begin to answer these questions, that is, to identify the factors which determine the abundance of this species and to examine the ecophysiological adaptations, such as dormancy, which may play a significant role in its distribution. The focus of this article is the determinants of abundance of *C. alexandra* and the implications for our current understanding of population regulation.

The System

Colias alexandra, first described by Edwards in 1873, is native to the Rocky Mountains and intermontane regions of North America. The taxonomy and distribution of the *C. alexandra* complex are discussed in detail by Brown (1973) and Ferris (1973). Discussions of other aspects of

the biology of this species can be found elsewhere, for example host plant preference (Ellis, 1973; Stanton, 1979), larval food plant use (Ae, 1958), adult nectar sources (Watt et al., 1974), and adult population structure (Watt et al., 1977).

The population examined in this study is univoltine (having one generation per year) and monophagous, utilizing only one larval food plant, *Lathyrus leucanthus* Rybd. (Leguminosae). In other populations *C. alexandra* utilizes other legumes and isolated bivoltine populations are known (Ellis, 1973; Hayes, 1981a, 1982). In the study population, females begin ovipositing in early July and continue through early August. Eggs are laid singly on the dorsal surface of the leaves of the food plant. Although specific egg distribution patterns have been associated with other so-called red-egg laying pierids (see Shapiro, 1981), there does not appear to be a consistent generation to generation pattern for this population of *C. alexandra* (Hayes, in prep.). No other Coliadine populations have been examined. There are two larval molts prior to the onset of winter conditions (i.e. regular nighttime freezing) in early September. In the third instar the larvae overwinter by entering diapause. Initiation of diapause is determined during the second instar as a response to cold temperatures ($\bar{x} \leq 24°C$; Hayes, 1982). Larval activity and development resume in late May, although the exact timing varies depending on weather conditions. There are two post-diapause or second season molts prior to pupation. Eclosion occurs in late June to early July, with males typically appearing earlier than females (Watt et al., 1977). The adults, and to a lesser extent the immature stages, may occur concomitantly with three other *Colias* species in this area: *C. scudderi, eriphyle* and *eurytheme*.

The Study Site and Field Methods

A relatively large population of *C. alexandra* occurs in the neighborhood of the Rocky Mountain Biological Laboratory (3200 m), near Crested Butte, Gunnison Co., Colorado. The population occupies fescue grassland/sagebrush habitats of the East River Valley (characterized by Langenheim, 1962). In order to accumulate information on the numbers and survivorship of *C. alexandra* during development from egg to larva to adult, a study plot was established in an area 13 kilometers southeast of Crested Butte along Brush Creek, elevation 2810 m, where adults and larval foodplant occur in relative abundance. This 20 x 20 m study plot is protected from grazing cattle by a three-strand barbed wire fence. The area actually surveyed encompasses 200 square meters, the vegetation within the plot being searched systematically in ten, 1 x 20 m strips. Plants with eggs or larvae are marked with numbered flags inserted into the ground next to them. A single plant usually provides adequate nutrition for a larva from hatching to diapause. Thus, individuals can be

followed to diapause by marking the location of the host plant. The survivorship, developmental rates, and activities of each egg or larva are monitored and recorded regularly at 48 to 72 hour intervals throughout the season. Post-diapause larvae are removed from the field plot and reared to eclosion in the laboratory. In this manner the incidence of parasitism, failure to pupate or eclose and the sex ratio can be determined. To avoid perturbing the study population, survivors were released at the study site. Post-diapause individuals outside the plot are observed to determine the incidence of predation and impact of inclement weather conditions. These basic techniques can easily be modified to conduct similar studies of other species.

Artificial populations can be created by releasing gravid females into flight cages (2x2x3 m) erected over natural vegetation. Adult *Colias* behave relatively normally within flight cages (Grula and Taylor, 1980; Silberglied and Taylor, 1972) and *C. alexandra* females oviposit freely (Hayes, 1981b). These artificial populations can be manipulated in a variety of ways without disturbing the natural population. For example, the effect of increased larval densities can be assessed by confining several ovipositing females at one time (Hayes, 1981b), or the effects of the presence of larvae of different ages on one another can be assessed by releasing gravid females into the cages at several-day intervals.

Wild-caught females will also oviposit under laboratory conditions. Although few matings have been obtained in the laboratory, *C. alexandra* have been reared successfully from egg to adult on a variety of host plants, clippings and an artificial diet (Taylor et al., 1981). Rearing within a controlled laboratory environment has facilitated the detailed study of several aspects of the behavioral ecology of *Colias* such as host preference (Stanton, 1979), food plant usage (Ae, 1958), and diapause dynamics (Hayes, 1982).

Results to Date

Age-specific or horizontal life tables were constructed for each year from 1975 to 1979 and 1981 (Table 1). The number of individuals entering each lifestage are recorded for each year. Age-specific life tables provide far more information than time-specific tables, but can only be used when a cohort is followed at close intervals throughout its life (see Southwood, 1976). In order to understand the effects that any one environmental factor has on population trends, a series of age-specific tables covering a number of generations is required. A number of different techniques have been used to analyze life table data in order to assess the effect of each component of the environment. The life table data for *C. alexandra* were analyzed by key-factor analysis techniques (Fig. 1; Varley and Gradwell, 1960). Key factor (also called K or killing factor) analysis is a concept originally introduced by Haldane (1949) and applied by Morris (1959)

Table 1.   Age-specific life tables for *Colias alexandra* (1975-1979, 1981).
           The population occurs 13 km southeast of Crested Butte,
           Colorado, elevation 2810 m.

| Stage | Number Entering Each Stage | | | | | |
	1975	1976	1977	1978	1979	1981
eggs laid	68	181	371	386	157	99
larvae hatching	42	108	277	259	97	17
second instar larvae	20	68	134	177	61	12
third instar larvae	8	36	87	128	32	8
diapause	4	22	32	37	21	—
post-diapause	2	1	6	5	—	—
adults	2	1	3	2	—	—

and Varley and Gradwell (1960) to statistical methods for identifying the
age-specific causes of population change. The k-value for mortality dur-
ing each life stage is the difference between the common logarithms of the
number of individuals entering that stage and the subsequent one. The
total generation mortality is calculated by adding all the k-values. The k-
values for each life stage over a number of generation are plotted against
time. The total generation mortality caused entirely or in part by a key
factor at a specific age can be seen by inspection of the inflections of the
curve (or statistically with limitation, see Smith, 1973) since its k-value
will change with time in the same manner.

I found that *C. alexandra*, like most insects, has a high intrinsic (or
inherent) rate of increase [r_m] and thus is capable of reaching large pop-
ulation numbers in a few generations. However, despite the vast potential
for egg production revealed under laboratory conditions or by dissection
of gravid females, in nature *C. alexandra* is vulnerable to numerous fac-
tors which act independently of its population numbers to keep the adult
population density relatively low. This is demonstrated by the fact that
survivorship to the adult stage is very low (mean survivorship = 1.2%, SD =
1.14; 1975-1979). The proportion of individuals which survive to adult
eclosion is relatively constant, thus the larger the number of eggs laid, the
larger the resulting number of adults. Key factor analysis of the data has
revealed that factors resulting in reduced natality appear to be the most
important in determining population trends. Natality is defined as a
measure of the ability of the adult females to yield their potential of fer-
tilized eggs (maximum potential natality is calculated by multiplying sex
ratio x number of adults x maximum egg production, Fig. 1). For this pop-
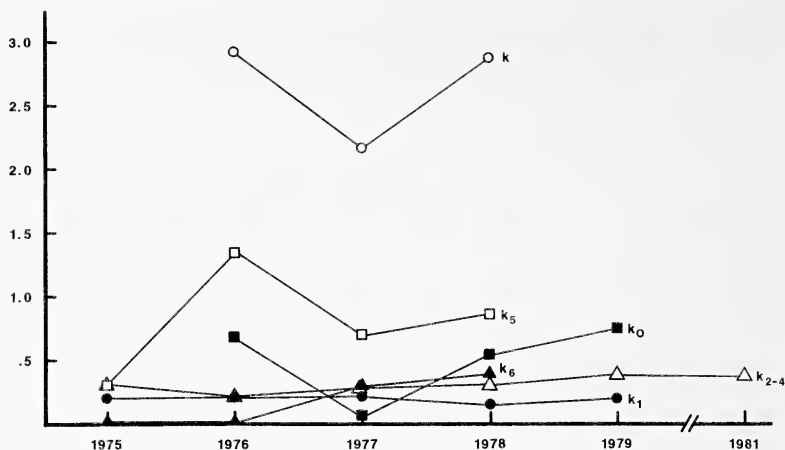
Fig. 1. Graphic presentation of k-factor analysis of life tables for *C. alexandra* 1975-1979, 1981. (k_0 = reduced natality, k_1 = egg mortality, k_{2-4} = pre-diapause larval mortality, k_5 = diapause mortality, k_6 = post-diapause mortality, K = total generation mortality.)

ulation of *C. alexandra* mortality during diapause (dormancy) may also be important, but egg mortality, pre-diapause larval mortality and post-diapause mortality contribute little to the total brood mortality. (In fact, pre-diapause larval mortality is highly negatively correlated to the population trend—a puzzling result which will hopefully be better understood through comparative studies of natural and artificial populations).

Among the factors which result in reduced natality and subsequent population depression are adult removal (e.g. through predation, over-collection, incidental loss to grazers), oviposition interference (e.g. poor weather conditions, interference by courting males) or reduced residence time (e.g. due to loss of nectar sources). The proportion of survivorship may be altered by unusual conditions (e.g. weather extremes, increase or decrease in predation or parasitism) between oviposition periods. These same trends (i.e. reduction of natality with corresponding overall reduction of population size) were found in a similar study of the pierid butterfly *Anthocharis cardamines* (Courtney and Duggan, 1983). A native of the British Isles and continental Europe, *A. cardamines* is a univoltine crucifer-feeding butterfly. Although based on fewer total observations (3 years), the type of data collected and method of analysis were nearly identical to mine. The fact that these techniques yielded similar results when independently applied to the study of a British species verifies the potential for a broader application of both the techniques and conclusions of this study to other species (e.g. Dempster, 1983).

The importance of natality in the study population of *C. alexandra* was

emphasized by incidental experimental manipulation when in 1979 about 30% of the young females in the population were removed (see Graham et al., 1980). As a result, in 1979 egg density in the study area was the lowest observed in the five year period (0.785 eggs/m², Fig. 2). The dramatic decrease in population density continued through the next two years. Climatic conditions alone during the two intervening seasons were probably sufficient to account for the further depression of population numbers observed; the number of eggs per unit area fell to 0.36 in 1981 (Fig. 2).

Concurrent with low *C. alexandra* densities during the 1981 season was the nearly explosive increase in numbers of the predaceous mite *Balaustium* sp. This free-living mite had only been previously observed in low numbers in the study area (e.g. Fig. 2; and Ae, 1958). Nymphs of *Balaustium* discover *C. alexandra* eggs, along with other relatively immobile prey items, during an apparently random or patternless search of vegetation surfaces. In 1981, a nearly two-fold increase in egg mortality was observed compared to other years and 65% of all pre-diapause mortality was attributable to this single factor. Year to year fluctuations in stage-specific mortalities of *C. alexandra* had been observed previously, but showed little effect on the overall population trends. However, it seems

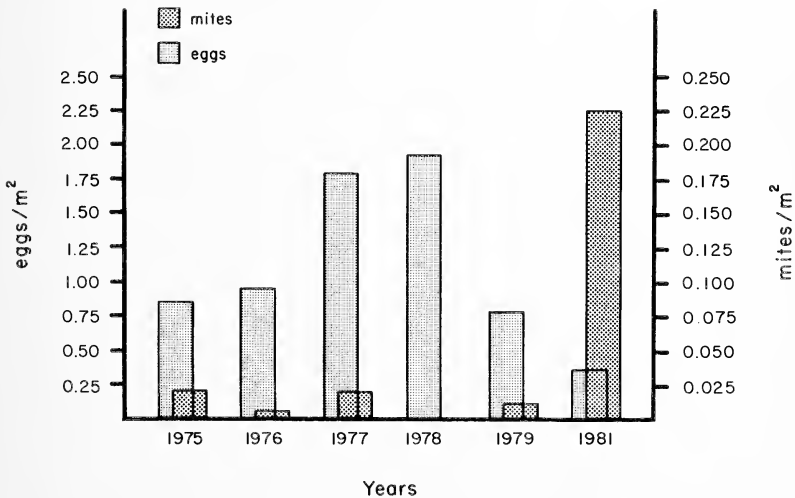Fig. 2.   Histograms for 1975-1979 and 1981 showing both the density of *C. alex-andra* as measured by eggs found on the larval food plant *Lathyrus leucanthus* in a 200 m² study plot (indicated on the left axis) and the corresponding density of *Balaustrium* as measured by maximum number of mites observed within the study plot during any census period over the season (indicated on the right axis).

likely that excessive egg loss under low density conditions may have a more drastic effect on subsequent population numbers.

The latter prediction is consistent with density dependent population regulation theory (e.g. May et al., 1974; Hassell, 1978). In this traditional view the most significant determinants of population size are factors whose influence varies with population density (e.g. predation). The theory predicts that a lower limit (or threshold number) exists, below which the impact of factors typically considered responsible for year to year population trends will not be important. Since the factors determining the abundance of the *C. alexandra* population are principally density independent (Hayes, 1981b), the findings of this study have important implications for the interpretation of population responses and extrapolation from these events to evaluate whether population regulation is density dependent or independent, or perhaps a combination (see reviews by Dempster, 1983; Strong, 1984).

Survivorship to the diapause stage in 1981 does not suggest any deviation from the typical proportional survivorship schedule of previous years (Fig. 2). A corresponding increase in adult numbers was observed in the field from 1981 to 1982 (W. B. Watt, pers. comm.) and 1983 (pers. obs.). In 1983, a mid-season survey of the population showed an increase in egg number ($> .48/m^2$ compared to the 1981 total of $.36/m^2$), despite the still relatively high mite numbers ($.2/m^2$), which had already caused at least 30% mortality (Hayes, 1984). These results thus fail to verify predictions of population regulation stemming from density dependent theory, but are consistent with my analysis of the 1975-1979 life table data in which variation in natality was identified as the key factor in determining the numbers of this butterfly population (Hayes, 1981b). The interactions of factors which contribute to reduced natality may be more complex than can be accounted for by our current simplistic density-dependent or -independent models of population regulation (e.g. Dempster, 1983; Strong, 1984).

It is very likely that an entirely different picture would have emerged from an examination of predator-prey interaction in 1981 alone, thus underscoring the necessity of long-term studies for the analysis of population dynamics. Despite the extreme effect of the mites on the egg number of *C. alexandra* in the field in 1981, their overall impact on the butterfly population is not significant. The occurrence of epidemic numbers of *Balaustium* was clearly independent of the depressed population number of *C. alexandra*. The opportunistic nature of this predator-prey interaction is evident in the effectively restricted predation by *Balaustium* of only the most immature eggs of *C. alexandra* in addition to the use of a diversity of resources such as pollen (Hayes, 1984).

The butterfly collector or researcher represents a relatively new type of predator to be considered. The analysis presented here suggests that the

extra removal of adults (particularly females) in some years can be devastating, even when population numbers appear to be high (e.g. Watt et al., 1979; also see Ehrlich et al., 1972). Another source of human disturbance is open cattle grazing, which is common throughout most of this region, although the specific effects of such practice on invertebrate populations are not well known. Certainly, the difference in vegetation itself between areas protected from grazing within my study enclosure and outside are quite striking. It may be that cattle have merely replaced the native ungulate herds which were once abundant in the area.

High mortality during egg and larval stages is typical for organisms collectively and simplistically referred to as "r selected" species, a term applied to those organisms which can be characterized by a suite of traits which are associated with high intrinsic rate of growth (reviewed by Stearns, 1976). Pre-adult losses may be as high as 99% of the total number of individuals entering the population (e.g. Dempster, 1973; Williams, 1975). The persistence of "r selected" populations is generally attributed to an environmental uncertainty which is faced by such populations and from which few individuals escape. The overall densities of "r selected" populations are well below the carrying capacity of their current environment and not determined by competition. Mortality due to environmental uncertainty operates in a density-independent fashion so that when any of the sources of mortality relax during the developmental stages, epidemic numbers may be reached in subsequent generations. On the other hand, if adult numbers are reduced (due to reduced natality in the case of *C. alexandra*) resulting in a smaller initial cohort, increased mortality during any developmental stage only contributes to depressing the population further. Populations limited by density-independent factors will therefore only recover slowly from sporadic changes in the mortality schedule.

Conclusion

The above study of *C. alexandra* provides insight into population level interactions (biotic and abiotic) of this species and can serve as a model for others. It is clear that we are only beginning to get a handle on the dynamics of the study population. If we are to achieve a clear perspective of the kinds of factors determining population numbers, populations must be followed for extended periods of time, not simply a few generations. All stages of the life cycle must be considered despite the prominance of a single stage, such as the adult butterfly, or the preeminence of a single mortality factor, such as the stage specific impact of the predacious mite feeding on the eggs of *C. alexandra*. Although five years of data are in many ways just sufficient to begin to draw meaningful conclusions, there are a few studies of such duration. The rapid decline of natural habitat, due to industrialization, urbanization and agricultural

practices, and subsequent loss of natural populations makes our task more urgent. It is only through the continued surveillance of such populations as the above that we can begin to interpret the impact of unpredictable perturbations, such as drought or fire, and the effect of the more predictable and manageable disturbances, such as collecting and grazing.

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Invited Paper

Sexual Selection and the Evolution of Butterfly Mating Behavior

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Abstract. The mating systems and courtship behavior patterns of butterflies are examined from the perspective of sexual selection theory. Particular attention is devoted to the effects of resource and female distributions on male mate-acquisition techniques and the occurrence and consequences of mate choice by males and females.

The study of butterfly mating behavior has a long history; most reports have been strictly descriptive, often anecdotal, or concerned primarily with the proximate mechanisms underlying courtship (for review: Scott, 1972; Silberglied, 1977). In the last few years, however, there has been an increasing effort to use butterflies and other insects to test current evolutionary hypotheses about the adaptive features of mating behavior (e. g. Blum and Blum, 1979; Thornhill and Alcock, 1983). The theory of sexual selection has been a guiding concept in this effort.

Sexual selection is the evolutionary process proposed by Darwin (1871) to explain traits whose primary function appears to be that of insuring an individual's success in courtship and mating. Of particular interest to Darwin were the elaborate secondary sexual characteristics displayed by males that in many cases seem likely to reduce a male's likelihood of survival. Darwin proposed that these traits are favored by sexual selection either because they increase a male's chances of winning contests for females with other males (advantage in intrasexual competition) or because they increase a male's chances of successfully seducing a female (advantage in intersexual choice). The brilliant colors of the males found in certain species of butterflies were interpreted by Darwin as a product of sexual selection, especially intersexual choice.

Beginning with Fisher (1958), but especially in the last 10 years, there has been an attempt to formulate the theory of sexual selection more precisely and to test more rigorously its predictions about male and female reproductive behavior. In this paper I will examine the mating behavior of

butterflies to see how well the observed patterns of diversity fit expectations derived from sexual selection theory and to suggest what data are needed to further test the theory.

Sexual Differences in Butterflies

In most species of animals females and the eggs they contain are a limiting resource for males (Bateman, 1948). This is because a female typically lays relatively few eggs during her life and need only mate once or twice to fertilize those eggs. Males, on the other hand, can cheaply produce sperm sufficient to inseminate many females. It follows then that males, but not females, should be active in searching out and courting mates since their reproductive success will be limited primarily by the number of eggs they fertilize, i.e., the number of copulations they obtain.

Trivers (1972) expanded Bateman's argument by pointing out that this difference between the sexes in reproductive strategy has its roots not only in the differences between the sexes in gamete size but more generally in the differences in parental investment between the sexes. In species in which males make a substantial investment in the offspring a sex role reversal is expected of a magnitude proportional to the size of the male's investment relative to that of the female (see also:Gwynne, 1983).

In recent years it has become clear that male butterflies provide more than just sperm to their partners. During copulation the male passes into the female's reproductive tract with the sperm a sizeable quantity (about 6 percent of the male's body weight) of accessory gland secretions that probably are of nutritional value to the female. These secretions are contained mostly in a cuticle-lined sac called a spermatophore and include proteins, lipids, hydrocarbons, and water (Marshall, 1980). The protein component of the male's secretions is definitely used by the females of several species of butterflies and moths for oogenesis and somatic maintenance (Boggs, 1981; Boggs and Gilbert, 1979; Boggs and Watt, 1981; Goss, 1977; Greenfield, 1982). A case has been made that the other components might also be of use to females (Marshall, 1982a). The secretions in spermatophores have not yet been shown to increase female fitness in butterflies but such an effect of spermatophores has been demonstrated in the Orthoptera (Gwynne, 1984). Mating with its concommitant production of secretion is costly to male butterflies in that it reduces male survivorship under certain conditions (Shapiro, 1982). There has been some argument about whether these secretions constitute a true parental investment (Alexander and Borgia, 1979); it is clear, however, that their selective consequences would be the same whether they are classified as parental or mating effort (Gwynne, in press).

In spite of this investment by male butterflies, females probably make a still larger investment in terms of allocation of resources to the eggs.

Therefore, sex roles in butterflies should generally conform to the classical form (males active and competitive, females coy and passive). However, sex role reversal might occasionally be expected, especially when males are selecting mates to give their investment or when females are limited by the availability of male nutrients (Trivers, 1972).

Butterfly Courtship and Mate Choice

Excellent summaries of the published information on butterfly courtship have been provided by Scott (1972) and Silberglied (1977) so I will here outline only the general pattern that has been observed. Once a male has located a receptive conspecific female, courtship follows in which the male is active and the female passive. If receptive and not already perched the female alights on vegetation or on the ground. The male then barrages the female with visual, chemical, and tactile stimuli by buffeting her with his wings or special scent-producing structures while flying near the female. Alternatively he may alight next to the female and perform a courtship display. In response, the female either remains motionless on the perch or extends her abdomen out from between the hindwings, thereby facilitating the act of coupling. The male then orients in a head-to-head position alongside the female and couples with her by curling his abdomen toward the female. Copulation follows and lasts from about 10 minutes to several hours (Shields and Emmel, 1973) depending in part on the average body size of the species, as shown for some pierids (Rutowski et al., 1983), and how recently the male has mated (Rutowski, 1979; Sims, 1979). During copulation the pair may engage in a post-nuptial flight either when prodded or sometimes spontaneously (Shields and Emmel, 1973). In sexually dimorphic species the sex that flies carrying the other generally has a coloration that more readily deters approaches and contacts by either conspecific males or predators (Rutowski, 1978b).

During courtship, the participants acquire information that is used in evaluating each other's potential as a mate. When copulation commits both males and females to metabolically costly investments sexual selection theory predicts that both sexes should engage in intersexual choice, that is, both should be sensitive to the quality, relative to conspecifics, of a potential mate. Females should be especially sensitive to a male's ability to produce secretions and males should be especially sensitive to female's ability to use the secretions profitably from their perspective (Rutowski, 1982a). This leads to two predictions. (1) Females should select among males on the basis of traits indicating that they can provide a large nutrient investment (Thornhill, 1976). A male's ability to produce these nutrients has been shown to be proportional to the time since he last mated and his size (Boggs, 1981; Rutowski, 1982a). Marshall (1982b) found male butterflies in the genus *Colias* collected in copulo were larger than those collected randomly. Among other traits that might be good

indicators of male quality in this regard are his age, courtship persistence, and chemical signals. Chemical signals might be especially important in that they are known to be critical for success in courtship in several species of butterflies (see Scott, 1972; Silberglied, 1977), and may be affected by larval (Grula et al., 1980) and adult diet (Schneider et al., 1975). Hence these signals might give the female critical information about the quality of a male's genes as well as the resources he has available to produce accessory gland secretions. Baker and Carde (1979) have discussed the possible role of sexual selection in the evolution of male scent-producing structures in moths.

The quality of the male's investment might be as important as its size. In ithomiine butterflies spermatophores contain defensive compounds sequestered by the male as an adult and used by the female in her own defense (Brown, 1984). These compounds are derivatives of the chemicals used in intersexual communication during the courtship (Edgar et al. 1976; Pliske, 1975a). This set of circumstances may be a product of sexual selection by females for males with chemical signals that indicate their supply of such compounds. A similar hypothesis has been proposed in Eisner (1980) and Conner et al. (1981) to explain the similarity between defensive compounds and male courtship pheromones in some other lepidopterans.

Female choice and its adaptive basis have yet to be directly tested in the butterflies although it is frequently invoked to explain phenomena such as female-limited mimicry. Turner (1978) has reviewed the literature on female-limited mimicry and analyzed the various explanations for the absence of a mimetic morph in males of species such as *Papilio glaucus* and *Speyeria diana.* He found sexual selection to be the most consistent with the current information on butterfly reproductive biology. Experimentation on female mate preferences will ultimately provide the best indication of the importance of mate choice in shaping male coloration. For example, Silberglied and Taylor (1978) have shown that females of the alfalfa butterfly *(Colias eurytheme)* mate preferentially with males whose wings reflect ultraviolet light, while the mate preferences of its congener *(C. philodice)* are not influenced by the presence of ultraviolet reflectance. Not surprisingly, the wing of *C. eurytheme* males strongly reflect ultraviolet while the wings of *C. philodice* do not (Silberglied and Taylor, 1973).

(2) Males should be selective in their choice of mates or at least their choice of courtship partner. If males are limited in their ability to produce these secretions then they should be choosy about who gets them. Marshall (1982b) found that females in field-collected mated pairs were heavier than females in a random sample from the same population. I have shown that males of the checkered white butterfly (*Pieris protodice*) preferentially court young females and large females (Rutowski, 1982b). Both these groups of females are expected to yield larger returns on the

male's investment than older or smaller mates. Young females have a longer life expectancy and female fecundity is related to size (Suzuki, 1978; Lederhouse, 1981). However, these are not absolute mating preferences for males will mate with highly receptive old or small females. But because they are less persistent in encounters with old or small females, this suggests that their behavior is structured in a way that reflects the costs and limitations of producing their investment.

While the information reviewed above suggests that mate choice may be occurring in butterflies a critical question surrounds its likely evolutionary significance. Do ecological circumstances in butterflies ever permit females and males to engage in effective mate choice? Obviously they must provide an individual with the opportunity to examine a variety of conspecifics without incurring undue costs in the form of time wasted or missed mating opportunities (Janetos, 1980). These costs will be minimized in species like *Colias eurytheme* and *Pieris protodice* that occur in relatively high density and whose flight seasons are not highly contracted, conditions that will not be met for all species of butterflies. Optimal conditions for choice are also not likely to be met at all times as density varies during a species' flight season.

Comparative Courtship and Investment Patterns

The nutrient investment made by male butterflies appears to have given rise to selection pressures that in turn have shaped the courtship behavior of males and perhaps females. However, the data that support this notion come primarily from a few species of butterflies in the pierid family. To what extent can these results be generalized to members of other families? Does interspecific variation in behavior reflect interspecific variation in investment? Obviously, this depends on a knowledge not only of the behavior of other species but also on a knowledge of the investments made by their males.

Male behavior in courtship varies among species (for review:Scott, 1972; Silberglied, 1977). At one extreme the male buffets the female briefly by flying about near her before alighting and attempting copulation. In the other extreme, the male performs special displays such as the bowing display of the grayling male (*Eumenis semele*, Tinbergen et al., 1943), the hairpencilling display of danaid males (Brower et al., 1965; Pliske, 1975b) or the wing waving display of *Eurema daira* males (Rutowski, 1983). During courtship a male grayling stands facing a perched female, bows forward, and clasps her antennae between his wings. The antennae, thereby, contact presumptive scent-producing scales on the male's wings. In danaid butterflies the male flies up and down in front of flying and perched females in a way that brings special scent-producing structures called hairpencils at the end of his abdomen into contact with the female's antennae. The barred sulphur (*E. daira*)

male alights next to a perched female and courts her by waving his fore-wing on the side next to the female up and down in front of her, actually rubbing the trailing edge of the wing along the length of the female's antenna with each upsweep.

These differences seem to be modest variations on a basic courtship plan found throughout the butterflies. The general lack of interspecific variation in the complexity of successful courtship suggests that interspecific variation in the magnitude of the investment made by males will be small. In contrast, Gwynne (1983) has observed a variety of courtship patterns in the Orthoptera that range from the standard male-male competition for females to situations in which females fight among themselves for access to males. In the species he observed, males pass nutrients to females at copulation and those species that display sex role reversal are those in which the male provides the female with huge quantities of secretion at mating, up to 20% of the male's body weight and more.

Recently, my coworkers and I surveyed the size of the investment made by males of ten species relative to their body weight and the body weight of conspecific females (Rutowski et al., 1983). The ten species included 5 pierids, 3 nymphalids, one papilionid, and one lycaenid. The courtships of these species are all similar in overall form. The results indicate a strong similarity from species to species in the quantity of nutrients passed by the male during copulation relative to his body weight. The size of the male's investment is consistently about 6% of his body weight. We conclude that these data support expectations from theory but acknowledge that some currently untested assumptions underlie this conclusion. Students of the mating behavior of butterflies and moths should pay special attention to species whose males exhibit unusually complex mating patterns or produce usually large or small nutrient investments.

These observations suggest that the diversity of courtship displays and signals found in butterflies is not a result of interspecific differences in the intensity of sexual selection but instead a result of differences in the direction of sexual selection favoring males that clearly announce their species identity or other characteristics that might enhance female reproductive success. That announcement of species identity is an important aspect of these displays is supported by the variation in courtship behavior observed in a complex of three small sulphurs, *Eurema daira, E. lisa,* and *Nathalis iole*, that are sympatric in the Neotropics and interact frequently. These species are similar in color; but, both *E. daira* and *N. iole* have a black bar along the trailing edge of the dorsal forewing that is not present in *E. lisa.* I have already described the wing-waving display of *E. daira,* and *N. iole* has a wing spread display that is dramatically different in form (Rutowski, 1981). In *E. lisa,* the male buffets the female with his wings in a non-specific way during the courtship (Rutowski, 1978b). Interestingly, the species most similar in coloration have the most

distinctive and pronounced displays. Suzuki et al. (1977) found a well-developed diversity in the courtship behavior of four similar species of *Pieris* sympatric in Japan. In mimetic complexes in which sexual and species discrimination by males and females might be a special problem as well as in complexes of similarly-colored sympatric relatives it is expected that male courtship signals and displays should be particularly divergent.

Female Mating Systems

Although female butterflies sometimes will mate multiply, as a rule they mate only one or a few times during their life (Burns, 1968; Ehrlich and Ehrlich, 1978; Pliske, 1973), and at widely spaced intervals (Suzuki, 1979). During their lives females are faced with the conflicting demands of mating, feeding, and ovipositing. A single copulation may take up a substantial percentage of the daylight hours during which temperatures are appropriate for flight. Copulation may have other costs as well such as exposure to predation. Time limitation on female reproductive output has been demonstrated for *Anthocaris cardamines* by Courtney and Duggan (1983) and for *Colias alexandra* by Hayes (1981) and suggested for other species by Rutowski (1978) and Wiklund (1982). Oviposition sites are characteristically widely scattered in space and females of most species deposit only a small complement of their total output of eggs at each oviposition site (Stamp, 1980). Egg dispersion maybe favored to reduce parasite infestations and overuse of larval resources. Nectar resources are similarly widely scattered, may not occur in the same areas as oviposition sites, and provide only a small quantity of material each time the female alights.

These observations lead to three predictions about female reproductive behavior in butterflies. First, mated females should be generally refractory to copulatory attempts in order to maximize time available for oviposition and feeding. This is in fact the case. Between matings females display a great reluctance to mate and a variety of movements and postures that mechanically impede male copulatory attempts. These include flutter responses (e.g. Rutowski, 1978b), mate refusal postures (e.g. Obara 1964b), and ascending flights that curtail male courtship attempts (Rutowski, 1978a). Both mechanical and hormonal cues initiated by the inflation of the bursa may be responsible for the initiation and maintenance of the female's refractory state (Sugawara, 1979; Obara, 1982). In heliconiine butterflies, females may use a chemical signal or antiaphrodisiac that is obtained from males during copulation to discourage the courtship attempts of other males (Gilbert, 1976). All of these behavior patterns may benefit a successful male by insuring that eggs produced using his nutrients are fertilized with his sperm. Last male precedence has been shown in several lepidopterans (Gwynne, in press).

Second, female butterflies should remate only when their supply of secretions or sperm from previous matings is depleted (Suzuki, 1979; Lederhouse, 1981). This appears to be the case in that the first-deposited spermatophore in twice-mated females is usually in a highly collapsed state (Rutowski et al., 1981). Studies of the patterns of female receptivity as related to supplies of sperm and male-imparted secretion are badly needed. Third, given that the secretions received from males are of nutritional importance to females, and that males are to some extent selective about who gets their secretions females are expected to sometimes play an active role in courtship. In fact, female butterflies have been observed to actively approach and chase males (courtship solicitation) especially when they are virgin (Wiklund, 1982) or when their supply of secretions from previous matings is depleted (Rutowski, 1980; Rutowski et al., 1982).

Male Mating Systems

Male butterflies are not monogamous but will mate repeatedly, even on the same day, if given the chance (Sims, 1979, Rutowski, 1979). Hence, polygyny best describes the typical male butterfly mating system. Emlen and Oring (1977) presented a model recently expanded by Thornhill and Alcock (1983) that relates the structure of animal mating systems to certain key ecological variables. They point out that in polygynous mating systems in which males display more or less classic sex roles, the strategies used by males to maximize contacts with females will be determined by (1) the distribution of receptive females in the environment and (2) the ratio of receptive males to receptive females, that is, the operational sex ratio. In the remainder of this paper I will present the predicted relationships between male mating system structure and these ecological variables and examine the extent to which butterfly mating systems do or do not fit the predictions.

Female- and Resource-Defense Polygyny. Emlen and Oring focus on the extent to which males can monopolize mates either through direct defense or through defense of resources of interest to females. If males can economically monopolize females by protecting them from the attentions of other males either in groups or individually in series female-defense polygyny will evolve. In butterflies no species is known in which females form defensible sex-specific groupings. In addition females become refractory after mating and remain so for some time. These factors will limit the benefits males may gain from female defense and suggest that this behavior will be rare in butterflies. No clear examples of female defense are known in the butterflies. However, in *Heliconius erato* the potential for such a mating system is strong in that males locate preemergent females using a chemical emitted by the pupae (Bellinger, 1954). Males might well defend these pupae. Why the pupae emits such a signal is unclear.

Males may also monopolize females by defending resources of interest to females and thereby gain exclusive copulation rights to females when they visit the resources. In the ecological circumstances that favor this system the resource of interest to females is clumped in a way that permits a male to be guaranteed frequent contacts with receptive females but to minimize time and energy in defense of the resource. In butterflies the primary resources of interest to females are nectar sources and oviposition sites. These resources are typically represented by small annual plants that are too widely dispersed to assure frequent visits by females many of which are likely to be unreceptive. Hence this mating system is also expected to be relatively rare in butterflies. When it does occur the resources should be found in clumps that are economically defensible and not too abundant, such as small trees and bushes.

As with female-defense polygyny, potential examples of resource-defense polygyny are rare as expected. Two cases stand out in which site defense appears to be closely tied to the location of appropriately structured resources. First males of *Papilio indra minori* participate in dramatic fights near service berry bushes, the prime nectar source for this butterfly in the region where the fights were observed (Eff, 1962). The hackberry butterfly, *Asterocampa leilia*, feeds as a larva on hackberry trees (*Celtis* spp.) which are characteristically small in stature. Males perch along washes and apparently defend stretches of the wash. Austin (1977) found that all such territories contained hackberry trees which might be prime locations for encountering ovipositing females. The hackberry trees would also be prime locations for encountering newly-emerged virgin females and so their defense might also constitute female-defense polygyny.

In some cases male butterflies also appear to be engaging in resource-defense polygyny but the resources are less obvious than oviposition sites or nectar sources. Males of the speckled wood butterfly (*Parage aegeria*) defend sun spots on the forest floor that Parker (1978) has suggested may be a thermoregulatory resource for ovipositing females. Davies (1978) in one of the most detailed studies of site defense in a butterfly has shown that males that defend sun spots have more frequent contacts with females than do males in other parts of the habitat. Wickman and Wiklund (1983) have confirmed many but not all of Davies' results and also shown that the intensity of sunspot defense increases with the likelihood of visits by females. In most of the territorial species discussed here the contests between males take the form of spiral, ascending flights.

Pure Dominance or Lek Polygyny. Resource defense mating systems are expected to evolve when a balance is struck between the arrival rate of receptive females and the density of would-be territory owners. If this balance is not met then mate monopolization potential is low and other types of mating systems are expected to evolve, either pure dominance

polygyny or scramble competition polygyny.

Male dominance or lek polygyny is only expected when the distribution of females in time and space is extremely widespread. Under these conditions selection may favor the evolution of traditional mating sites that are not based on any resources of interest to the female (Bradbury, 1981). At such sites males are expected to aggregate and may defend territories in anticipation of visits by receptive females. If territories are defended at these traditional mating sites they will not be centered on any resource of interest to the female and the aggregation of males is referred to as a lek.

The defense of hilltop territories by male butterflies is well known to butterfly collectors and students of butterfly behavior (see Shields, 1967), and clearly supports the expected relationship between lek polygyny and ecological variables. Typically the most hotly contested territories are those nearest the top of the hill and contain neither larval foodplants nor nectar resources. Lederhouse (1982) has documented hilltopping behavior in the black swallowtail, *Papilio polyxenes*. As well as showing that males are territorial on hilltops he has shown that the highest territories are most likely to be visited by receptive females and intruding males and most actively defended. A similar relationship between territory position and attractiveness to males has been shown for the great purple hairstreak, *Atlides halesus* (Alcock, 1983). In both *P. polyxenes* and *A. halesus*, as expected, the food resources are widely distributed and the flight season is very protracted, often lasting several months (Lederhouse, 1982; Alcock, 1983).

The symbolic territories that characterize leks need not be contiguous. In such situations the lek territories are dispersed and most likely to occur in areas where males can get the best view of passing females or in areas females are likely to visit due to habitat structure. In *Heodes virgaureae* (Douwes, 1975), *Inachis io, Aglais urticae* (Baker, 1972), *Incisalia iroides* (Powell, 1968), *Precis coenia* (Scott, 1975a; Hafernik, 1982), *Lasiommata megera* (Dennis, 1982), *Vanessa atalanta* (Bitzer and Shaw, 1979), *Nymphalis antiopa*, and *Polygonia comma* (Bitzer and Shaw, 1983), males occupy and apparently defend for several days sites that have been described as being along wood margins, along paths, in ravines, or in bare areas. As an alternative interpretation such areas could be construed as resources in the form of space for optimal movement through the environment and, hence, the behavior of the males could be taken as resource defense polygyny. In either case, the ecological circumstances expected to give rise to such a mating system would be similar.

At this point it is appropriate to make four comments on territoriality in butterflies. First, the occurrence of territoriality in butterflies has been disputed (Scott, 1974; Suzuki, 1976) largely because of difficulty in distinguishing sexually motivated chases from aggressive chases and because the lack of an obvious resource near a male's perching site. More

recent studies (see especially Wickman and Wiklund, 1983) firmly document that territoriality and aggression do occur in butterflies. Second, territorial behavior no doubt intergrades into non-territorial behavior within and between species. In some species perching sites appear quite labile in time and space (Scott, 1975a; Hafernik, 1982; Suzuki, 1976). Third, observations of territorial behavior have generally been lumped under the name of perching or waiting by males for purposes of mate location (Scott, 1974, 1975b, 1982). The scheme presented here helps understand the variation in territorial behavior and the ecological circumstances that favor such behavior. More detailed studies of perching are needed that focus on the relationship between male behavior, resources, females, and the spacing of individuals in the environment. Finally, males engaged in contests for access to females are subject to intrasexual selection for traits that maximize success in such contests. This type of selection has been promulgated by Silberglied (in press) as an alternative to intersexual mate choice used by Darwin (1871) as an explanation for the brilliant color found on males but not females of some species of butterflies.

Alcock (in press) has also found that some hilltopping butterflies are non-territorial and only patrol the hilltop. He like Parker (1978) has suggested that such behavior will be most advantageous when the ecological circumstance favor traditional mating sites but the density of conspecific males at the site is too low or too high to make exclusion of conspecifics profitable at these sites. If there are only a few males on the hill, territoriality makes little sense for individuals; if there are many males on the hill the energetic costs of excluding them will make territoriality disadvantageous.

Scramble Competition Polygyny. Abundant but not patchily distributed resources and short flight seasons will favor males that do not engage in contest competition with other males for females at resources or leks but that instead fly about the environment searching for receptive females in a scramble competition with other males. Two types of scramble competition polygyny have been proposed.

When receptive females are highly concentrated in time and space males should aggregate in high density when and where these aggregations are likely to occur. Emlen and Oring have called these aggregations explosive breeding assemblages. Such concentrations of receptive females are not likely to be common in butterflies but the mating frenzy of monarch butterflies (*Danaus plexippus*) that occurs just before they disperse from their winter aggregations may qualify as an explosive breeding assemblage. Females in these aggregations become receptive during the days before they disperse in the spring and during this time males fly about courting females and mating with any that will have them (Hill et al., 1976; Brower et al., 1977). Also, concentrations of reproductively active non-territorial males near food sources have been described for

Eumenis semele (Tinbergen et al., 1942) and *Perrhybris pyrrha* (DeVries, 1978).

Thornhill and Alcock have suggested that prolonged searching polygyny will evolve when none of the conditions discussed above are met. Males then are expected to fly about broadly in search of receptive females in an effort to outrace their competitors. From the information and analysis given above this is perhaps the most likely mating system to be found in butterflies. It is the most commonly reported form of butterfly mating-locating behavior reported in surveys by Scott (1974, 1975b, 1982). Males engaged in scramble competition for mates characteristically fly rapidly through the environment and investigate anything they contact that even remotely resembles a female. Such males are often seen to closely investigate larval foodplants where they may encounter newly emerged virgin or receptive ovipositing females.

There are two additional comments on sexual selection and male mating systems in butterflies. First, competition for access to females has frequently been invoked to explain the observation that in any given flight season males typically eclose earlier than females. This is called protandry and several theoretical and empirical analyses support an intrasexual competition explanation (Wiklund and Fagerstrom, 1977; Wiklund and Solbreck, 1982; Iwasa et al., 1983; Parker and Courtney, 1983). Furthermore, Singer (1982) has presented data suggesting that males in univoltine species with restricted flight seasons may be under more intense sexual selection for protandry and therefore may, as a result of the required rapid development, be smaller than females than males in, for example, multivoltine species (see also, Lederhouse, et al., 1982). Second, although this discussion has focused on interspecific differences in male mate acquisition strategies, variation in mating system structure may also occur within species. The possibility of such variation has been discussed by Scott (1974, 1982) who cited a number of species in which males patrolled in some areas and perched in others. Male mate-locating behavior also varied with time. He focused on the role of population density in determining the optimum mate-location strategy. Dennis (1982) has documented changes from patrolling to site defense in the wall brown (*Lasiommata megera*) and attributes the change to changes in resource distribution as well as density. Investigators of butterfly mating systems should be sensitive to the fact that as in other species of insects intraspecific variation in male mating behavior may occur along the axes of male size (Alcock et al., 1977), time of day (Marshall, 1982b), population density (Cade, 1979), or other relevant ecological variables.

The existing information on butterfly mating systems appears to provide preliminary support for the theoretical relationships predicted by sexual selection theory between mating system structure and various ecological variables, especially the distribution of females and the operational sex ratio as both are influenced by female mating and

emergence patterns. However, there is much more to be done. Quantitative assessments of female and resource distribution, and careful comparative studies of detailed case histories will go far toward establishing the accuracy of these correlations.

Summary

Clearly, the most robust tests of sexual selection theory will come from testing explicit predictions drawn from it using butterflies and other organisms. Butterflies appear to be particularly suitable for tests of predictions about sexual differences and mating systems because of the unusual nature of male nutrient contributions made during mating and because of the diversity in male mating behavior found both within and between species. I hope this article serves to introduce some of this potential to butterfly biologists and stimulates additional interest in the adaptive features of the sexual behavior of these beautiful and behaviorally diverse organisms.

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Some Observations on Spatial Distribution in a Montane Population of *Euphydryas editha*

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Abstract. Counts of montane *Euphydryas editha* along transects at Almont Summit, Colorado, show that males form a dense aggregation along a ridgetop with an estimated 30:1 (male:female) sex ratio. Fertilized females showed preference for subsites below the ridgetop at least as rich in oviposition plants but less rich in nectar resources, where the sex ratio was close to 1:1. Mark-release-recapture data suggest mating is less probable on the ridgetop than below it. This suggests the possibility that non-aggregating males, at least under conditions similar to those of 1983, may have greater reproductive success than those in aggregations, raising questions about the function of such aggregations.

Recently it has been suggested that the availability of fertilizable females is the link between ecological factors and mating systems in butterflies (Odendaal et al., 1984). Several tentative hypotheses were advanced about the characteristics of mating systems in populations with short and long periods of female availability. The assumption was made that the duration of female availability in butterflies is largely determined by the length of the period in which the larvae will have access to suitable resources.

Odendaal et al. used Nearctic checkerspot butterflies of the genus *Euphydryas* (Nymphalidae: Nymphalinae) as exemplars of explosive breeders, since time for development of their larvae is, in general, severely limited by the growth cycle of their larval food plants. For such butterflies, Odendaal et al. predicted, among other things, (1) synchronization of female emergence so that their availability is short, (2) a strong tendency for males to form dense aggregations where the structure of the population is "open" (i.e., where resource or other constraints do not concentrate individuals in relatively restricted areas), (3) relatively little spatial overlap between males and fertilizable females, (4) an operational sex ratio (OSR) biased toward males in the mating area and (5) little

choosiness by males in selecting mates. We tested some of these hypotheses in a Colorado population of *Euphydryas editha* during the summer of 1983.

Materials and Methods

Near Almont, Gunnison County, Colorado, *E. editha* forms diffuse colonies between about 2700 and 3000 m in sagebrush-dominated meadows where the larval food plant, *Castilleja linariifolia*, a hemiparasite on sagebrush (*Artemisia*) and appropriate nectar resources are available (Ehrlich and White, 1980). A concentration of these butterflies at Almont Summit (2800-3000 m) has been under study since 1976 (Holdren and Ehrlich, 1982). To determine the distribution of the two sexes, we used mark-release-recapture (MRR) techniques (Ehrlich and Davidson, 1960; Brussard, 1971) and transect counts (see Pollard, 1977). A total of 3400 m of transects were established (Fig. 1). One 350 m transect followed a dirt road along a ridge at 3000 m, above a topographically diverse slope (Fig. 2). Other transects crisscrossed three benches cascading from the ridgetop and separated by steep slopes, unsuitable, or marginally suitable habitat.

The distributions of the larval host plant, *C. linariifolia* and various nectar resources were mapped. The latter included primarily *Senecio integerrimus* (the one on which most nectaring is observed regardless of the relative abundance of flowers), and secondarily *Erigeron* sp. early in the season, and, as the *Erigeron* senesced, *Wyethia amplexicaulus*. We also recorded the collective distribution of *Taraxacum officinale*; *Agoseris glauca*, another yellow composite; *Allium textile*; and *Pseudocymopterus montanus*; all of which were occasionally visited for nectar. To determine plant distributions, we estimated abundances along each 50 m segment on a scale of 0 (absent) to 3 (abundant). By averaging the estimated abundances of the 50 m segments comprising the ridgetop and three south-southeast facing benches fanning out below it, distributions were roughly evaluated in these four main areas where more than ¾ of the butterflies had concentrated (Table 1). Because all four areas include segments lacking abundant resources, none received an average rating of 3.

The transects were walked by both of us simultaneously in varying patterns and directions on 11 days between 23 June and 18 July. The 350 m transect along the road was walked eighteen times (once on six days, twice on four days and four times on one day), and other transects were walked on alternate visits. The counts for the less frequently walked transects were corrected by multiplication to the standard of the road transect (e.g., one walked nine times had its count doubled). Where *Euphydryas* were common, one of us observed while the other recorded. Effort was made to maintain a pace of 2 s/m, except where butterflies were very
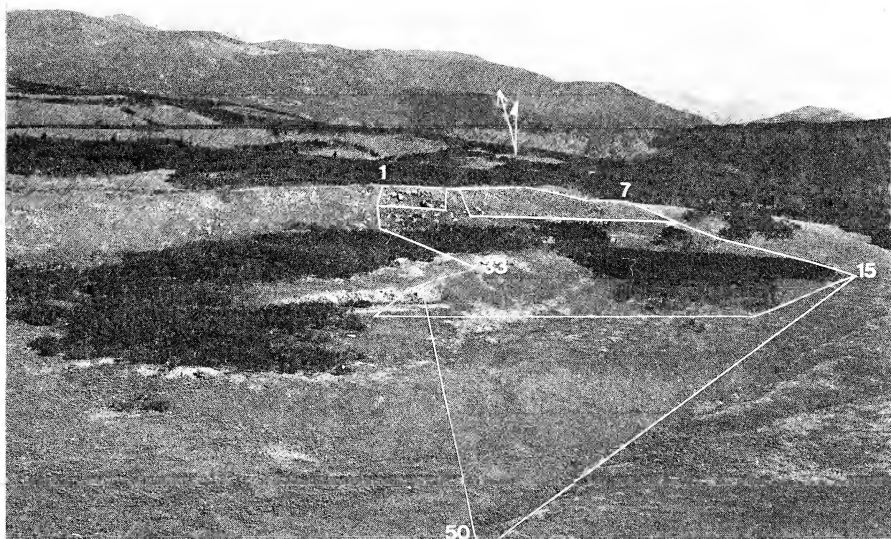
Fig. 1.   Aerial photograph of Almont Summit, Gunnison Co., Colorado showing transects.

Fig. 2.   Close-up aerial photograph of Almont Summit, Gunnison Co., Colorado, showing road and benches (33 is on first bench, second bench is at furthest left point on transect).

Table 1. Summary of *Euphydryas editha* (using corrected numbers), oviposition plant and nectar source distribution at Almont Summit, Colorado, determined during transect counts, June-July, 1983.

Site	TOTAL SEEN Male	Female	% OF TOTAL Male	Female	% OF SEX Male	Female	RATIO Male:Female	FOOD* Plant	NECTAR* Resources
Road	543	18	.499	.017	.581	.117	29.5:1	2	2-2**
1st Bench	180	25	.165	.023	.192	.161	7.2:1	1	0-1
2nd Bench	11	14	.010	.013	.012	.092	.8:1	1	0-1
3rd Bench	81	69	.074	.063	.089	.444	1.2:1	2	0-1
Remaining Sections	118	30	.108	.028	.126	.186			
Total	**933**	**156**	**.856**	**.144**	**1.000**	**1.000**	**1.000**		

*0 = none seen
1 = plants scarce
2 = plants common
**First number refers to *Senecio integerrimus*
Second number refers to secondary nectar resources

scarce. In those areas the pace was roughly twice as fast, but the obser-
vations of both of us were recorded. In practice, this means *E. editha* were
recorded if they were present within about 2.5 m on either side of the tran-
sect. For more than 99 percent of these sightings the sex was recorded
as well.

In addition, during 7 visits to the site (between 2-18 July) a total of 167
male and 53 female butterflies caught along the transects were given
individual marks using standard techniques and released. These marked
butterflies were included in the transect counts.

Results

Both larval host plant and nectar resources are distributed over much of
the area in the vicinity of the transects (Fig. 3). *Castilleja linariifolia* was

Fig. 3.   Distribution of larval host plant and nectar resources along transect.
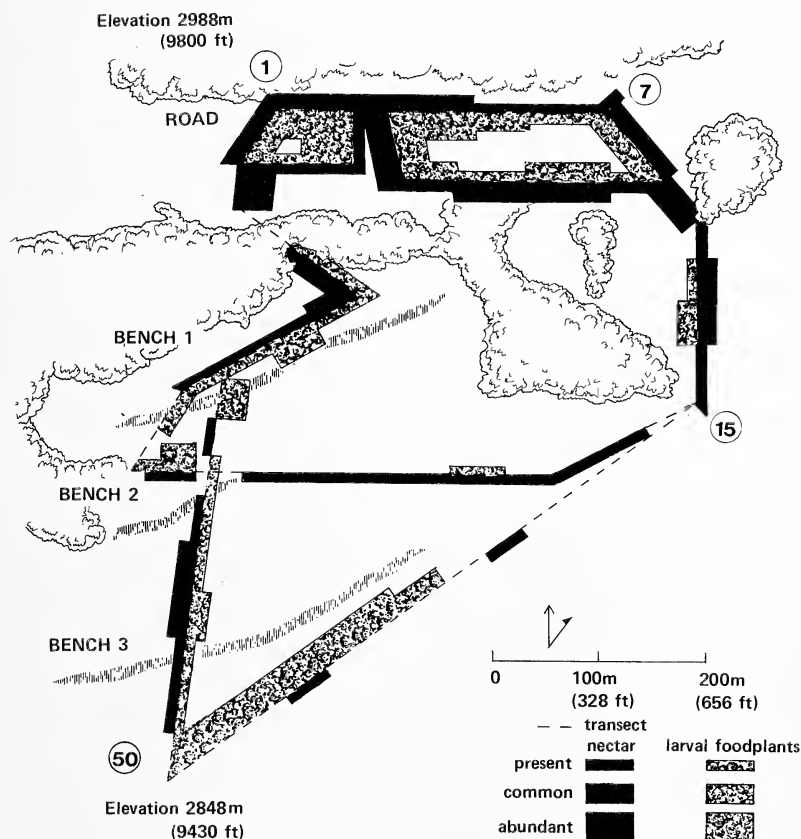
more common along the third bench than along the ridgtetop, and more common on the ridgetop than on the first and second benches. Primary nectar resources were abundant along the ridgetop, scarce on the first bench, absent on the second, and scarce on the third. Similarly, secondary nectar resources were common along the road and less common to scarce along the benches (Table 1).

Distribution of the two sexes is shown on the map in Figure 4. The data presented in the figure accords well with our subjective evaluation of their relative abundance in different areas.

While individual *E. editha* could be seen throughout most of the area, Table 1 (using corrected numbers) lists the estimated distribution by sex and the ratio of males to females found in the four preferred areas. We found that males tended to form a dense aggregation along the ridgetop. During transect walks, an average of 29 individuals were seen along the 350 m ridgetop section compared with 22 individuals along the remaining 3050 m of transects criss-crossing the site. Females, in contrast, were found primarily on the third bench.

Recapture data confirmed male movement into but not out of the area of aggregation. During each walk of the ridgetop transect an average of 64% of the catch were first-time captures. Yet, of the 61 males recaptured there, 55% were caught within 50 meters of their original capture. Furthermore, of the 104 males marked in the ridgetop aggregation, none were later seen on the third bench.

Recapture data showed no female movement into or out of the area of male aggregation. We could not determine where most matings occurred, but we assumed larval hostplants on the third bench were preferred for oviposition, because 44% of the females seen during the transect walks (using the corrected numbers, see Table 1) were found there.

Discussion

That selection has favored synchrony of female availability in *Euphydryas* is indicated by the temporal patterns of oviposition. Females emerge with a large complement of eggs, and, at least in central California populations for most years, only larvae from the earliest two masses have the opportunity to develop to diapause. In addition, in laboratory experiments, the size of these early masses is unaffected by foraging prior to oviposition (Murphy, et al., 1983). The phenology of the oviposition plants in the montane population at Almont Summit (Holdren and Ehrlich, 1982) would also appear to place a premium on early emergence and oviposition.

Our results also indicate that female fitness depends upon the availability of oviposition plants in suitable condition, and that selection should favor males that emerge early enough to mate with early emerging females. We first observed females on 23 June, and the only two virgin

females were seen on the first and third benches on 25 June and 8 July. All females seen after 15 July had wear ratings greater than .75, indicating they were not newly emerged (Ehrlich et al., 1984). By that time inflorescences of *C. linariifolia* are usually fully opened.

As in *E. chalcedona* (Murphy, 1983; Murphy et al., 1984) *E. editha* distribution and nectar resource availability correlate: the primary source, *Senecio integerrimus*, was most abundant along the ridgetop where males were concentrated; available, although very diffusely, on benches where females were most common; and generally absent where butterflies were thinly scattered.

The hypothesis of Odendaal et al. that there should be relatively little spatial overlap between males and fertilizable females is supported by our data (Fig. 4). Detailed investigations of other populations are needed, however, since, for example, in the Jasper Ridge C demographic unit, the
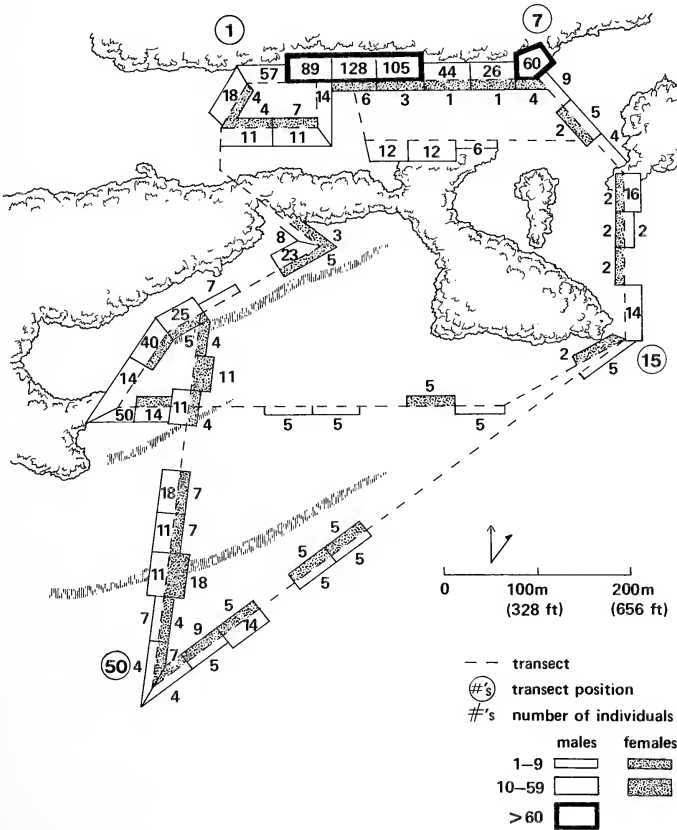

Fig. 4. Distribution of *Euphydryas editha* by sex along transect.

casual impression is that the sexes are largely co-distributed. Walking the transects at Almost Summit did not provide sufficient observation of either virgin females or matings, and assessment of the fertilizability of non-virgin females was not possible, (Labine, 1968; Ehrlich and Ehrlich, 1978). The two virgins seen were located on the first and third benches, while the matings occurred on the road, first bench and between the second and third benches. Transects were walked at a pace which may be too fast to detect teneral, flightless virgins, and were walked between 10:00 and 13:00 when virgins could be scarce if, for example, emergence were normally in the early morning or late afternoon, and most matings occurred immediately.

The choice of oviposition plant at Almont Summit is determined in part by the phenologies of the "suitable" alternatives (Holdren and Ehrlich, 1982) and it is likely that there is higher survivorship of early as compared to late egg masses, as is the case for this species at Jasper Ridge (Singer, 1972). Selection therefore might favor not only early emergence, but also prompt mating and quick oviposition on closest suitable larval host plants. Females eclosing on the benches (where males are relatively scarce) and not immediately mated there may attempt to move toward the ridgetop where mating is assured. Such movement may be discouraged by the woodland barrier separating the lower benches from the ridgetop (Fig. 1), and further delay mating and oviposition.

The proportion of males leaving the area of aggregation (rather than simply perishing there) remains to be determined. This determination may prove difficult in a population with such an open structure.

The operational sex ratio (the ratio of sexually active males to fertilizable females) at Almont Summit is clearly different in the two putative mating areas. On the ridgetop it is highly skewed toward males; on the third bench it is not. In addition, determination of the OSR must consider the variability of male sexual activity (males may emerge still sexually immature) and the fertilizability of non-virgin females.

And, of course, there remains the problem of determining exactly what prompts the male aggregation if, because of the skewed OSR, the chances of mating on the hilltop are not higher than below. The abundance of nectar is a possibility, but individuals spend much of their time perched on the road surface and flying out at passing objects.

If oviposition is preferred on the third bench and just enough males remain there to provide first and second matings, then the OSR on that bench may show a bias towards females. In this protandrous species that bias could increase over time as female emergence becomes predominant (see Iwasa et al., 1983). Thus, the suggestion of Odendaal et al. that the OSR in the mating area is heavily male-biased, may well be true for the ridgetop (if that is where most matings occur), but not for the third bench. Presumably, in both areas, the evolutionary importance of access to those

females decreases over time.

Finally, although the hypothesis that males should show little choosiness in mates was not formally tested, our observations support it. Chasing behavior is the response of male *E. editha* to moving objects, be they virgin or fertilized females, males of the same or other species, or even other flying insects, birds or shadows. Its modification into mating behavior may rest largely on the acquiescence of the butterfly pursued.

Clearly the most important data needed for rounding out the picture of mating strategies in this *E. editha* population is determination of 1) the mating success of males within and outside of the aggregation; 2) the proximate reason for the aggregation; are males attracted primarily to the nectar sources, to the warm, bare road on which they perch, to the presence of other males, or to a combination of these (or other) factors; 3) patterns of sexual activity in males, and 4) fertilizability in non-virgin females. We intend to start investigation of all of these points in the 1984 field season.

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Inheritance and Frequency of a Color Polymorphism in *Danaus plexippus* (Lepidoptera: Danaidae) on Ohahu, Hawaii

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Abstract. A distinct color polymorphism has been observed in the Monarch butterfly *Danaus plexippus*, on Oahu, for at least the last 19 years. The rarer white morph, approximately 4% of the populations sampled in recent years, has grey-white rather than orange scales, but the pattern of its black scales is indistinguishable from that of the normal orange morph. Genetic crosses indicate that the white morph is homozygous for an autosomal recessive allele.

It is hypothesized that the white morph persists in Hawaii because it is not at a selective disadvantage to the orange morph in the presence of predators. Both morphs are captured by avian predators here in Hawaii, either because the milkweed on which the monarch larvae primarily feed (*Calotropis gigantea*) is low in or lacks certain cardiac glycosides, or because their principal vertebrate predators, *Pycnonotus* spp., are less susceptible to cardiac glycosides than other birds.

Introduction

Polymorphism, defined by Ford (1953), is the occurrence of two or more discontinuous forms of a species within one habitat in such proportions that the rarest form cannot be maintained solely by recurrent mutation. Examples of balanced and transient polymorphism are numerous in the Lepidoptera. Some of them involve Batesian mimicry of unpalatable species. Among the most famous examples are the transient polymorphism of *Panaxia dominula* L. (Fisher & Ford, 1947) and the transient and balanced polymorphism of *Biston betularia* L. (Kettlewell, 1958).

Color polymorphism has also been observed in the genus *Danaus*. Ford (1936) reported that Lamborn (1924) and Van Someren (1924, 1925) have studied the presence or absence of a subapical bar in the forewings of both sexes of *Danaus chrysippus* L. More recently Mitchell (1966) reported a "color" polymorphism in *Danaus plexippus* L. on Oahu, Hawaii.

Although the pattern of the black scales is indistinguishable in the two Hawaiian forms, the ground color of males and females of the white morph is cream-white to light-grey rather than orange. These mutants are depicted in Riotte and Uchida (1978). Urquhart (pers. comm.) noted "faded monarchs" during his studies of migration of *Danaus plexippus*, but did not consider them polymorphs. Faded areas on the wings of these monarchs can also be induced by microcauterizing the prismatic pigmented maculae of the pupa (Urquhart, 1972). Clarke and Rothschild (1980) worked with a mutant form of *Danaus plexippus* in which the adults possess areas of "whitish yellow" ground color. The ground colors of these two forms do not resemble that of the white monarchs found in Hawaii.

This paper reports on an investigation of the mode of inheritance of the white morph in Hawaiian *D. plexippus* and examines some of the possible selective factors that may have caused the high frequency and the increase in frequency of the white morph in Hawaii.

Methods

Crosses were carried out in the winter and spring of 1980, in the spring of 1983 and winter of 1983-1984, using adults that emerged from pupae collected from milkweeds (*Calotropis gigantea*) on the campus of the University of Hawaii. When their wings had dried following emergence, males and females were paired to effect the desired crosses. Pairs were kept in 40 cm x 26 cm x 30 cm wooden frame cages with top and sides constructed of either clear plastic or fine plastic screen that allowed sunlight to enter. The adults were maintained on a 10% sucrose solution. Eggs laid within the cages were removed on a fine paint brush, placed on fresh milkweed leaves, and put into petri dishes or vials until the larvae hatched. Larvae were allowed to feed on the leaves and grow to the third or fourth instar; they were then transferred to 30 cm x 15 cm x 10 cm plastic boxes. The boxes were examined and fresh leaves were fed to the larvae at least five days each week. Upon pupation, individuals were transferred from the larval containers into wooden frame cages. Newly emerged adults were removed from the cage and isolated to prevent mating. All rearing and mating cages were kept on a bench near a west facing window in broken sunlight in a well ventilated, non air-conditioned room.

A total of 23 crosses were initiated of which 16 produced a new generation of adults. Most larvae raised in the lab in the spring of 1980 and 1983, and a high proportion of larvae in the field were infected with a cytoplasmic polyhedrosis virus, and as a result only a small number of eggs were successfully raised to adults in the laboratory each generation. In the winter of 1983-84, only small numbers of eggs were obtained in most crosses, but larval mortality was very low.

Information concerning developmental times (egg, larval, and pupal

stages) was recorded for all F_1 and F_2 members in 1980.

Inter-year comparisons of the relative abundances of white and orange morphs were based on our own collections and data obtained from Mitchell (1966). Mitchell's data were based on "over 600 monarchs" reared from larvae and pupae he collected in Waianae and Hawaii Kai, Oahu, in February 1965. Our data were obtained by raising 522 pupae collected on the University of Hawaii campus (approx. 40 km E of Waianae and approx. 12 km W of Hawaii Kai) during the winter and spring of: 1972-1973, 1979-1980, 1980-1981, and 1982-1983; and in the winter of 1981. Monarchs become abundant in November-December and become inconspicuous around food plants by May or June each year on Oahu (Etchegary & Nishida, 1975).

Results

The white morph appears to follow a simple Mendelian mode of inheritance for an autosomal recessive allele (Table 1). All white-white crosses (crosses 1, 2, A) yielded only white offspring. The crosses between field orange and F_1 white individuals (crosses C, D, E, K) all produced orange offspring which were presumably heterozygotes. Crosses between white individuals and presumed heterozygotes (crosses F & G) yielded both white and orange offspring in ratios which were not significantly different from 1:1. Crosses H, I, and J only produced orange offspring.

The orange-white crosses of 1980 (crosses 3 & 4) gave rise to a mixture of both white and orange individuals. The orange individuals used in these crosses were probably heterozygotes. This would explain the near 1:1 ratio of white to normal coloration. Heterozygotes constituted about one-third of the field population in any year since 1972, assuming Hardy-Weinberg equilibrium (Table 2), so it is not improbable that the normal female and male in crosses 3 & 4 were heterozygotes. Very few individuals were produced by the one successful cross between two heterozygotes (cross L), but the occurrence of both white and orange offspring is consistent with the interpretation that the white allele is recessive.

Since the numbers produced by a cross are small, phenotypic ratios in filial generations are not known with any certainty. The heavy mortality of larvae may have altered the proportion of the white:orange ratio in 1980 if one morph was more susceptible to the virus than the other.

Times required for completion of the three main developmental stages were compared between the morphs in the 1980 crosses. Since no homozygous orange line was established, the duration of the egg stage of orange individuals was estimated by using the length of the egg stage for all eggs from white-orange crosses. No statistical comparison was performed on the length of the egg stage of the two morphs. Non-parametric statistical tests were made between the lengths of the larval developmental stages of the two morphs and no significant differences were found by a

Table 1. Results of crosses between laboratory reared *Danaus plexippus.* Parents were derived from pupae collected in the field or derived from laboratory crosses, except the white female of cross B which was collected in the field as a mated adult. Crosses 1-4 were performed in 1980, and crosses A-L were performed in 1983-1984.

Cross	Male	Female	Orange Male	Female	White Male	Female
1	White field	x White field	0	0	2	3
2	White F_1 of cross 1	x White F_1 of cross 1	0	0	3	2
3	White field	x Orange field	2	3	1	5
4	Orange field	x White F_1 of cross 1	1	3	7	3
A	White field	x White field	0	0	26	24
B	Unknown	x White field	19	15	19	14
C	White F_1 of cross B	x Orange field	7	6	0	0
D	Orange field	x White F_1 of cross B	7	3	0	0
E	White F_1 of cross B	x Orange field	6	8	0	0
F	Orange F_1 of cross B	x White F_1 of cross B	11	5	8	4
G	White F_1 of cross B	x Orange F_1 of cross B	6	8	8	5
H	Orange field	x Orange field	37	37		
I	Orange field	x Orange field	8	10		
J	Orange F_1 of cross H	x Orange F_1 of cross H	0	2		
K	White field	x Orange field	10	12		
L	Orange F_1 of cross K	x Orange F_1 of cross K	4	2	1	

Table 2. Abundance of the white morph of *Danaus plexippus* in Oahu populations. Genotype frequencies are based on Hardy-Weinberg assumptions.

Date	Sample Size	Number White	Genotype NN[a]	Frequencies Nn[b]	nn[c]	Allele Frequency n
1965* (Feb)	600	3	0.863	0.132	0.005	0.071
1972 (Nov-Dec)	67	2				
1973 (Feb)	33	3	0.628	0.329	0.043	0.208
1973 (May)	16	0				
1979 (Dec)	43	2				
1980 (Jan)	42	2	0.681	0.288	0.030	0.175
1980 (Feb)	61	1				
1980 (Mar)	18	0				
1980 (Dec)	21	5				
1981 (Jan)	131	2	0.635	0.324	0.041	0.203
1981 (Feb)	77	3				
1981 (Mar)	13	0				
1981 Nov-Dec	177	6	0.672	0.294	0.034	0.180
1982 Dec	134	6				
1983 Feb-Mar	101	6	0.599	0.350	0.051	0.226

* Mitchell (1966)
a NN = orange, homozygous dominant
b Nn = orange, heterozygous
c nn = White, homozygous recessive

Mann-Whitney test. However, when the duration of the pupal stages were examined a significant difference was noted between the two forms at the 5% level. Since laboratory conditions were not carefully controlled with this type of comparison in mind, the significant difference noted between morphs in lengths of the pupal developmental periods cannot be accepted uncritically. There were no differences in the developmental periods between males and females within each of the two morphs.

Estimates of the frequency of white morphs on Oahu were obtained from Mitchell (1966) and from our own data and range between 0.5% and 5.1% (Table 2). Zimmerman (1958) estimated the earliest arrival of monarchs to Hawaii to be around 1845 when milkweeds were introduced; he made no mention of the existence of the white morph in Hawaii as of 1958.

A 2×4 $\times^2$ contingency analysis was performed to determine if the proportion of white morphs differed among the periods: 1965, 1972-73, 1979-80, and 1980-81. The test showed significant differences among the periods in the proportion of white individuals (p<0.01). When the 1965 data were compared against those for the combined periods of 1972-1973, 1979-1980, and 1980-1981 by a 2 x 2 contingency text, $\times^2$ was again significant (p<0.001). When a comparison was made among the years 1972-73, 1979-80, and 1980-81 by a 2 x 3 contingency table, no significant difference was found. Each of these tests is statistically independent of the other. From these results it appears that the ratio of white to orange has increased since 1965, but has not changed significantly during the last decade.

Discussion

The results of the crosses performed in this study indicate that the white trait is inherited as an autosomal recessive, similar to the observations of Clarke & Rothschild (1980) also in *Danaus plexippus*. However, Clarke & Rothschild suggest that the light morph they studied has a lower fecundity than the normal morph, whereas no pleiotropic effect has been documented in the Hawaiian white morph.

The analysis of phenotype frequencies indicates that the white morph may have increased between 1965 and the 1970's. There is some uncertainty about the increase because of the different sites sampled by Mitchell (1966) and ourselves. The proportion of white monarchs has probably increased since 1958, since it was not reported in Zimmerman's (1958) extensive monograph on Hawaiian insects, and because the earliest dates of collection of white specimens in 3 local museums are: 1965, 1967 and 1976. Since no change in frequency is apparent between 1972-1973 and 1982-1983, the genotype frequencies may have reached a balanced polymorphism. There is no evidence of any pleiotropy, differential mating, alteration of selection pressures, or heterozygote advantage which could explain the observed shift in gene and genotype frequencies. Matings between the two morphs have been observed in the field.

This white morph is evidently not restricted to Hawaii. A similar morph has appeared in Queensland, Australia (De Baar, 1982) and has been described for *Danaus plexippus* ssp. *erippus* from Argentina by Clarke & Rothschild (1980). Clark (1932) mentions that a specimen which may have been the white morph was captured outside the National Zoological Park in Washington, D. C. in 1896 by Capt. Robert Gill. Clark described

the specimen as, ". . .rather larger than usual and was entirely white on both sides."

The rarity of this white morph in North America may be due to predation on white individuals soon after emergence, because they are not recognized by vertebrate predators as unpalatable. Until recently the campus study sites and low altitude areas of the Hawaiian Islands have lacked avian predators which would eat larvae, pupae or adults of large lepidoptera such as monarchs. Since the spring of 1978, however, two bird species have appeared in numbers on the campus of the University of Hawaii and have been seen attacking larvae and orange and white adult monarchs in the area of campus milkweed stands. These birds, red-vented bulbuls (*Pycnonotus cafer*) and red-whiskered bulbuls (*Pycnonotus jocosus*), were first observed on Oahu in the mid-1960's (Berger, 1972). However, the bulbuls have actually never been seen ingesting the larval or adult monarchs. The wings are usually broken off the butterflies before the bird leaves the attack site carrying the adult body, possibly to nestlings. Both the white and normal orange monarchs are attacked in flight or at rest by the bulbuls. Thus, in Hawaii, it may be that both the mutant white individuals and the normal orange individuals have an equal probability of surviving to reproduce.

The observation that bulbuls attack both white and orange morphs suggest that both obtain insufficient cardiac glycosides from the local milkweed (*Calotropis gigantea*) to make them unpalatable to predators, or that *Pycnonotus* spp. are not susceptible to cardiac glycosides as in the case of grosbeaks (Fink & Brower, 1981). Preliminary analysis of the tissues of white and orange monarch butterflies raised on *Calotropis gigantea* in Hawaii indicate cardiac glycoside (cardenolides) concentrations are in the range of 140-180 ug/0.1 g of dry tissue (James Cohen, pers. comm.). This level in monarch populations of some geographic areas (Mexico, Massachusetts) is not quite sufficient to cause vomiting in in blue jays, the standard bio-assay animal (Fink & Brower, 1981).

The selective advantage conferred by the white allele which has allowed it to increase to a frequency of 20% is unknown. The maintenance of the white allele in the Hawaiian population is probably due to the fact that white individuals are not at a selective disadvantage here, whereas they may be at a selective disadvantage in North America, where they would be rare, unfamiliar to predators, and so killed despite having cardiac glycoside defenses.

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A New Species of *Narraga* Walker (Geometridae, Ennominae) from Georgia, with Biological Notes

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Abstract. *Narraga georgiana*, n.sp., is described from Ohoopee Dunes, Tattnall Co., GA, and contrasted to other known N. American *Narraga* species. *N. georgiana* is a day-flier, and the only member of the genus known to occur east of the Mississippi River. The food plant is shrub goldenrod, *Chrysoma pauciflosculosa* (Michx.) Greene (Compositae). Immature stages, habitat and habits of *N. georgiana* are described.

Introduction

On April 11, 1981, the last two coauthors were collecting butterflies together in the Ohoopee Dunes, which straddle the Candler and Tattnall county line midway between Macon and Savannah, Georgia. They noticed a small, erratically flying moth crossing the dirt road they were following, and collected 9 specimens within 30 minutes. Unable to identify the moth beyond the family level, Finkelstein sent specimens to Covell for determination. Based on the brown color, bipectinate antennae, and striking pattern of the hindwing underside, the moths were identified as members of the genus *Narraga* Walker, 1862 (= *Fernaldella* Hulst, 1896). Comparison of superficial and genitalic features of a lengthy series of the Georgia moth with specimens of other *Narraga* material from Texas and westward has convinced us that the former represents a new species, which we name and describe as follows:

Narraga georgiana Covell, Finkelstein & Towers, new species

Description: Head with vertex mixed dark brown and ochre. Front bulging, clothed with rough scales, mixed dark brown, ochre, and whitish. Palpi project forward; segments 1-2 white with a few brown scales; apical segment dark brown. Antenna broadly bipectinate in male, narrowly so in female; shaft and pectinations clothed dorsally with dark brown and ochre to whitish scales, appearing peppered; underside of shaft and pectinations black, unscaled.

Thorax dark brown dorsally with some scattered ochre to whitish scales; patagia brown with conspicuous whitish outer basal patch. Underside mostly whitish with some brown scales. Legs mostly mixed dark brown and ochre, with extensive whitish scaling on outer side of coxa and femur. Hind tibia bears 2 spurs in both sexes.

Abdomen dark brown, peppered with ochre; segments 1-7 banded apically with mixed ochre and white, the bands interrupted middorsally with ground color.

Wings broad, shaped as in other *Narraga* species (Figs. 1-4). Ground color evenly dark chocolate brown, fading to paler brown in older specimens. Forewings above unmarked except as follows: variable diffuse ochre scaling in basal area along costa, diminishing inward in density; diffuse ochre patch along costa at top of median area; sharp ochre bar, slightly curved, extending inward from costa near apex; and ochre checkering in fringe. Hindwings above uniform dark chocolate brown, including fringe.

Forewings beneath have markings of upperside repeated, but apical area and upper terminal area dominantly ochre. Curved bar near apex silvery pale yellowish white, edged with brown. Silvery yellowish white terminal bars, edged with dark brown, occupy spaces between veins R_4 and R_5, R_5 and M_1, and M_1 and M_2; traces of narrower bars occur between M_2 and M_3 and M_3 and Cu_1 in some specimens. Pale checkering in fringe also more silvery yellowish white than above.

Hindwings beneath dominantly ochre, the dark chocolate brown restricted to variably wide edging around silvery yellowish white spots and lines; brown shading usually widest toward base. Basal half of wing usually has 5 variably shaped silvery yellowish white markings, basad of median line: long basal costal edging, followed by broader spot near top of median line; trapezoidal basal bar followed by small subtriangular spot in cell; and large spot near inner margin, sometimes extending to base, though mixed with ochre and dark brown. Median line irregular and variable, usually with bulges just above middle, and again at inner margin; line divided between bulges into 2 separate sections in some specimens examined; and several specimens seem to have line broken into 3 parts. Usually 7 rounded dashes between veins toward outer margin, although the largest (third from apex) occupies much of the space between M_1 and M_3, crossing vein M_2. Fringe checkered ochre and brown, with small white patches opposite some of the terminal white dashes.

Wingspan: males, 1.9-2.1 cm; females, 2.3-2.6 cm.

Wing length: males, 1-1.2 cm; females 1-1.3 cm.

Male genitalia (Fig. 9) small; 1.1-1.3 mm from tip of uncus to tip of vinculum. Tegumen thin, circular. Uncus broad at base, narrowing to ventrally directed point. Juxta broad, bilobed, membranous. Valves deeply cleft; lobed valvula only slightly indented at about midpoint of ventral margin, just beyond 2-3 small, setose tubercles; sacculus very broad with slightly ragged margins, ending in rounded point. Aedoeagus very broad and membranous at anterior end, narrowing to a curved point; dorso-distal end developed into a rounded tooth (carina). Usually 2 small, narrow, pointed cornuti in the vesica.

Female genitalia (Fig. 11) about 3.2-3.5 mm in length. Sterigma membranous, posterior half slightly narrower than anterior half; rounded notch in middle of posterior margin, with slight projections of margin on each side of notch. Ostium rounded, leading into short, moderately sclerotized ductus bursae which narrows slightly as it blends into curved neck of corpus bursae. Corpus bursae entirely membranous, simple, with ductus seminalis entering it near juncture with ductus bursae. A single, very small, thorn-like signum present at about midpoint of corpus bursae.

Types: Holotype male, Ohoopee Dunes, Tattnall Co., Georgia, Sept. 11, 1981, leg. I. L. Finkelstein (C. V. Covell, Jr. genitalia preparation no. 1,112). Allotype

female, same locality and collector, Sept. 6, 1981. Both in American Museum of Natural History, New York City. Paratypes: 17 males and 10 females, all from the type locality, Apr. 11, 1981 (4 males), Sept. 6, 1981 (7 males, 6 females), Sept. 11, 1981 (6 males, 3 females); and Apr. 13, 1982 (1 female). Paratypes in the Carnegie Museum, Pittsburgh; Florida Collection of Arthropods, Gainesville; University of Georgia, Athens; Natural History Museum of Los Angeles Co., Calif.; U.S. National Museum of Natural History, Washington, D.C.; and collections of the authors. Preserved ova, larvae, and pupae in U.S. National Museum.

Discussion

Ferguson *in* Hodges *et al.* (1983) applied *Narraga* Walker 1862 to 2 North American species formerly considered to be in *Fernaldella* Hulst, 1896. The type of *Narraga* is *Geometra cebraria* Huebner (a synonym of *Phalaena fasciolaria* Hufnagel) from Europe; that of *Fernaldella* is *fimetaria* Grote & Robinson, 1870, from Texas. The other included species is *stalachtaria* Strecker, 1878. In order to establish the identity of *fimetaria*, a search was made for the 11 specimens mentioned in the original description, all of which were sent to the authors by Belfrage, who collected them in Texas in August. Only one specimen was located that might be one of these syntypes: a male from the New York State Museum in Albany. Labels on this specimen include one with the number "4085" and another in what seems to be Grote's handwriting (in the opinion of Dr. Timothy McCabe), stating "Fidonia fimetaria Gr.-Rob., Texas, ♂." Since it is not labelled "Type," it may or may not be part of the type series. The most distinctive superficial characteristics of *N. georgiana* are the larger size in all specimens examined and more uniform and darker brown upper wing surfaces than any specimens of *N. fimetaria* examined.

Examination of the genitalia of the Texas male (C. V. Covell preparation #1169) and other presumed *N. fimetaria* reveals a distinct thumb-like process at about midpoint along the ventral margin of the valvula of the valve (Fig. 10), where only a slight indentation occurs in *N. georgiana*. The sacculi of the two species also differ: that of *fimetaria* is distinctly more narrow than that of *georgiana*. In the female genitalia, the posterior margin of the sterigma in *N. fimetaria* is not notably notched, and lacks the pair of posteriorly directed protuberances characteristic of *N. georgiana*.

In the other North American *Narraga* species, *N. stalachtaria* Strecker 1878 (type locality, Rio Navajo, Colo.), the wing coloration is almost entirely yellowish, with brown usually restricted to the upper part of the terminal area of the forewing, and along outer margin of the hindwing. The male genitalia are similar to those of *N. fimetaria*, but the valvula seems to have a more narrow thumb-like process, and the sacculus is more rectangular, with dorsal and ventral margins more nearly parallel. The female genitalia appear much like those of *N. fimetaria* in the limited material studied.
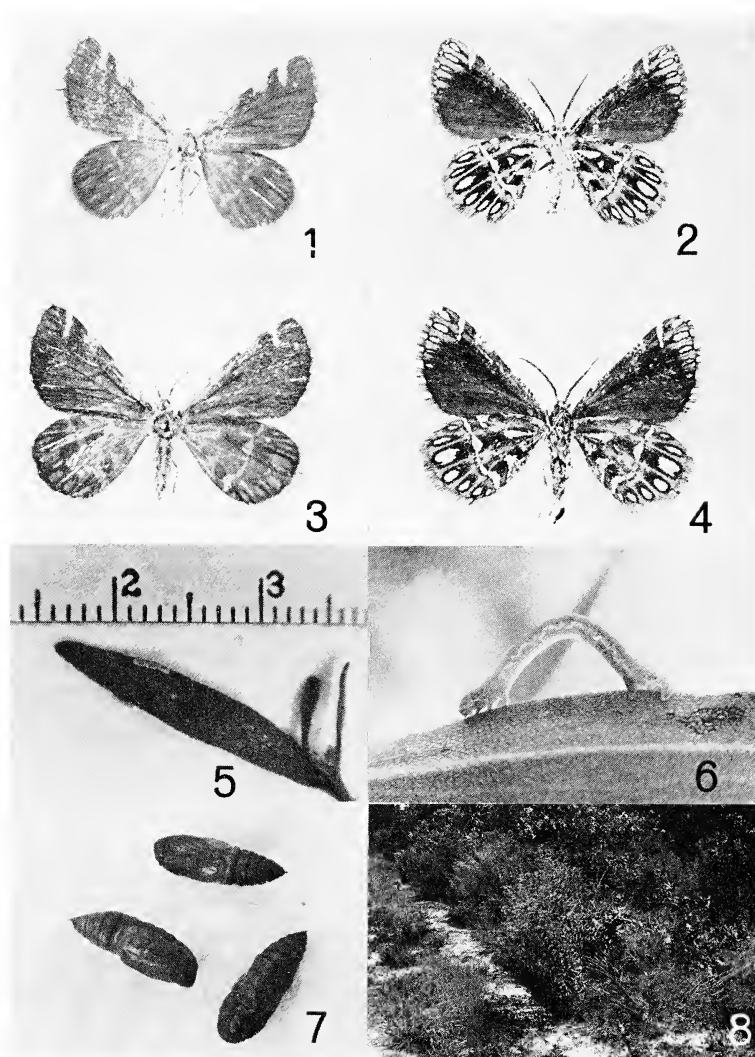
Fig. 1. *Narraga georgiana*, n. sp., paratype male, upperside.
Fig. 2. *N. georgiana*, n. sp., paratype male, underside.
Fig. 3. *N. georgiana,* n. sp., paratype female, upperside.
Fig. 4. *N. georgiana,* n. sp., paratype female, underside.
Fig. 5. *N. georgiana,* n. sp., ova on leaf of shrub goldenrod, *Chrysoma pauciflosculosa* (Michx.) Greene.
Fig. 6. *N. georgiana*, n. sp., fifth instar larva on leaf of shrub goldenrod.
Fig. 7. *N. georgiana,* n. sp., pupae.
Fig. 8. Habitat of *N. georgiana,* n. sp., Ohoopee Dunes, Tattnall Co., GA, Sept. 11, 1981. Note foodplant, shrub goldenrod, in bloom (center).

   N. georgiana is known only from the type locality and a similar habitat 5
miles north in Emanuel Co., GA. *N. fimetaria* is known to occur in Texas,
Kansas, Iowa, Arizona, Colorado, Utah, Nevada, Montana, Idaho and
California. *N. stalachtaria* is known from New Mexico, Colorado,
Wyoming and Oregon. *N. georgiana* appears to be double-brooded (as is
N. fasciolaria in Europe), with adults flying in April and mid-July to mid-
September. Known flight dates for *N. fimetaria* are May and late June to
the end of August; those for *N. stalachtaria* include May, June and August.
The meager locality and temporal data on hand at this time make firm
statements regarding range and flight dates of the two western species
risky. However, preliminary evidence would seem to indicate that all three
species are at least bivoltine.

Life History

   On 6 September 1981, individuals of *N. georgiana* at Ohoopee Dunes
were observed in close association with a flowering shrub later identified
as shrub goldenrod, *Chrysoma pauciflosculosa* (Michx.) Greene (Com-
positae). Although not seen ovipositing on foliage of this plant, the moths
flew close by concentrations of it, and were not found where the plant was
absent. Live female moths and cuttings from shrub goldenrod were taken
to Atlanta, where oviposition on the leaves was observed over the next 3
days. Ova were most commonly placed in chains along the leaf margins (Fig.
5), less often singly in the middle of either the dorsal or ventral leaf surface.
The ova are oblong, dorsoventrally flattened, about 0.8 mm in length.
They appear grayish green with a silvery sheen, and the surface appears
smooth with a slanted grid pattern faintly discernible under 40X
magnification. After 3 days the eggs darken, and eclosion occurs on the 6th
or 7th day.

   There are 5 larval instars. The caterpillars are about 2 mm in length upon
hatching and about 5 mm at the first ecdysis, and are blackish and hair-thin
at this stage. They will accept both young and older leaves of shrub
goldenrod immediately, eating patches in the upper epidermis. Molting to
the 2nd instar occurs after 5-6 days. The color of the 2nd instar is dull
medium to dark green with a smooth surface. When not feeding or moving
about, the caterpillars stand erect at about a 30°-40° angle from the
foodplant surface, closely resembling young leaves. Molting to the 3rd
instar occurs at 12 days after eclosion, when the larvae are about 8 mm
long. Color in this instar becomes more bluish green than in the 2nd instar,
but similarity to the foodplant color is still close. In this instar the
caterpillars begin to feed inward from the edges of the leaves, consuming
the whole thickness of leaf material. Molting to the 4th instar occurs at the
18th day after eclosion, and the larvae are from 12 to 14 mm long and about
1.5 mm wide. The color is still a uniform green, but paler than in the 3rd
instar. Grainy, irregular, yellowish green longitudinal striations are now

apparent. After 23 days the larvae molt to the 5th instar (Fig. 6), and achieve a maximum length of 23-24 mm by the 28th day. Color is still green in this instar with the yellowish striations increasingly wider and more pronounced as the larvae age. A wider, irregular yellowish lateral line may be present. The color and mottling of the larvae are very similar to those of the foodplant, providing excellent camouflage.

On the 30th day after eclosion, larvae began leaving the foodplant and wandered for 4-5 hours about the container in which they were confined. As they wandered they began to shorten and widen, eventually becoming quiescent, having shortened in length to 10 mm—less than half their maximum length of 24 mm. These prepupae also became increasingly mottled with bluish and brown, and the yellowish striations disappeared. Some burrowed into the sand at the bottom of the container, while others became quiescent without burrowing. Those that burrowed made a loose cocoon of sand cemented with silk. Pupation occurred between 24 and 36 hours after the larvae became quiescent.

The pupa (Fig. 7) is green at first, but soon becomes dark brown. Length is 8 mm, with a 0.25 mm cremaster. Emergence of the first imago was on the 21st day after pupation; most of the others emerged on the 23rd day. Reared adults averaged slightly smaller than wild-caught specimens, and also emerged between 30 October and 6 November 1981, when conditions outdoors would be inappropriate for adult activity. We believe that in nature the late-summer generation overwinters in the pupa stage, and is normally on the wing in April. While 83 larvae entered the 5th instar, only 19 pupated; and of these only 8 emerged as adults (5 of them deformed). This poor survivorship was probably due to the fact that the foodplant used for this rearing was collected along with the parent females, and was kept in a refrigerator during the entire life cycle, and was increasingly poor in quality as time passed. On 13 April 1982 more specimens were collected at the original site, and also at another habitat in Emanuel Co., GA, 5 miles north of the other locality. Four females from the Tattnall Co. site were kept alive and taken along with living plants back to Atlanta, where the plants were placed in pots, and the females confined for oviposition. They lived for 7-8 days, and deposited 135 ova on detached leaves. This time the leaves with ova attached were pinned to leaves on the potted foodplants, and the plants were placed outdoors in a screened enclosure. In contrast to the gestation period for the late summer ova kept indoors the previous season, with hatching 6-7 days after oviposition, the April ova eclosed between the 9th and 17th days. Other details of the life history were as described above, but with the spring rearing, mortality rate in the 5th instar was considerably reduced over that experienced in late 1981 (probably because of the living foodplants). At least 81 larvae in the second rearing pupated, and 63 adults emerged between June and October. These adults were comparable in size to wild-caught individuals,

and few were deformed, testifying to better rearing conditions than in the fall 1981 group.

On 27 August 1982 a full-grown larva of *N. georgiana* was found eating foliage of shrub goldenrod at Ohoopee Dunes, confirming that plant species as a natural foodplant of the moth. The larva was reared to the adult stage in captivity. Known foodplants for other *Narraga* species include other Compositae only: *Artemisia campestris* L. for the Eurasian type species, *N. fasciolaria* (Hufnagel) (Prout *in* Seitz, 1912), and *Gutierrezia dracunculoides* (DC.) Blake for a Bell Co., Texas, specimen of *N. fimetaria* (Grote & Robinson) (data from specimen in U.S. National Museum).

Ecological Notes

The type locality of *Narraga georgiana* is a unique area of elliptical sand dunes that are thought to be of Pleistocene origin (Wharton, 1978), located along the Ohoopee River in Tattnall Co., GA. It can be reached by leaving Rt. US 1 at Lyons and proceeding northeast on GA Hwy. 152 to a point ¼ mile east of the Ohoopee River crossing. There one follows an unmarked dirt road that runs diagonally to the left, and takes the first dirt road on the left from that one. The first *N. georgiana* were seen between 500 and 700 yards from that intersection.

The habitat (Fig. 5) of "deep coarse sands" supports the following vegetation: ground cover of British soldier lichens; herbaceous plants such as sand spikemoss, nailwort, sand chickweed and *Balduina angustifolia* (Pursh); shrubs such as rosemary, red basil, blue flowering woody mint, jointweed and shrub goldenrod; and dwarfed trees, dominantly longleaf pine and turkey oak (Wharton, 1978).

The moths were observed flying only in open areas in bright sunlight between 10:30 AM and noon, virtually disappearing after noon as temperatures rise. Most moths stayed within 18 inches of the ground, and exhibited slow but erratic flight. They alight abruptly with wings folded together over the back, resting on twigs, blades of grass or other vegetation. No individuals were found in a search of nearby wooded areas. They remained close to patches of their foodplant, and diminished in numbers as foodplant individuals became more sparse. As no night collecting was attempted, it is not known if *N. georgiana* will come to lights.

material in that museum; and Dr. Tim L. McCabe, N.Y. State Museum, Albany, for lending material.
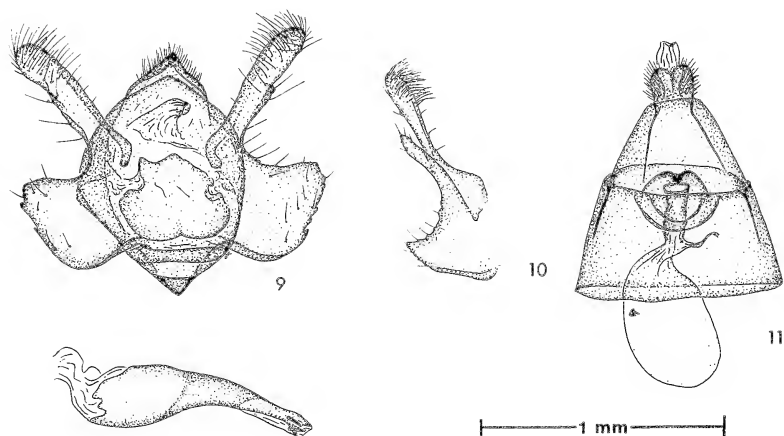
Fig. 9. *N. georgiana,* n. sp., male genitalia.
Fig. 10. *N. fimetaria* (Grt. & Rob.), left valve of male genitalia.
Fig. 11. *N. georgiana,* n. sp., female genitalia.

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Book Reviews

Hilfsprogramm für Schmetterlinge. Ökologie und Schutz von Tagfaltern und Widderchen.
Blab, Josef and Otakar Kudrna, Naturschutz Aktuell No. 6, 1982. Kilda-Verlag. 135 pages. Price: DM 14,80, paperback.

While this rich little volume is intended as a "helpprogram" for German butterflies, it is additionally an impressive review of German butterfly species, their habitats and host plant associations. But in the "red book" tradition, this is primarily a catalogue of tragedy, describing a condemned fauna cascading in a seemingly unstoppable decline, a conservation job too big. Despite lacking the autecological appeal of British and American treatments of endangered species, this book breaks from recent pattern in trading species-by-species dike-plugging for a community consideration of butterfly conservation, i.e., covering entire habitat types (fenlands, grasslands, alpine areas, etc.) and their associated butterfly species.

Indeed, the Germans have little choice as theirs is a rapidly vanishing fauna, from which even the most abundant and widespread European butterflies are disappearing. A valuable companion atlas to the *Hilfsprogramm* is *Fundortkataster der Bundesrepublik Deutschland* (Harald Schreiber, part 2: Lepidoptera 1976. Schwerpunkt Biogeographie, Universitat des Saarlandes, Saarbrucken), which documents present and historical distributions of butterflies throughout Germany. Converting the atlas maps to numbers is sobering. Melitaeine butterfly distributions are typical; for example, *Melitaea cinxia* is extant in 66 10x10 km quadrats, but has been lost in 121 quadrats from which it had been recorded previous to 1960; hence it survives in but 35% of its rather recent historical range. Likewise, *Melitaea phoebe* survives in 46% (31 of 68 quadrats) of its range, *M. athalia* 46% (119 of 261), *M. didyma* 39% (41 of 105), *Euphydryas aurinia* 42% (59 of 83), *E. maturna* 18% (13 of 71), and *E. cynthia* 7% (1 of 14). This is particularly distressing since knowledge of the natural history of German butterflies seldom extends beyond host plant associations, and rarely provides even a superficial explanation of butterfly population structure and regulation.

Nonetheless, the findings of the *Hilfsprogramm* are consistent with more quantitative studies. Not surprisingly, half of those species identified by Blab and Kudrna as threatened are affected by intensification of meadow and pasture uses; more surprising is that fully one-third are threatened by "mining" operations. Besides identifying the obvious threat to butterfly populations of habitat conversion, these authors also support the notion that overcollecting can impact populations. The Old World, in fact, has become an archipelago of well-known collecting sites, ravaged year after year by hordes of lepidopterists. Just how long can Austria's Bluntautal, Spain's Campo Real, and Morocco's Ifrane absorb the culling without a substantial loss of species including those that are neither rare nor highly localized? (Contrary views of collecting as a threat are offered in German language reviews of this book by Eitschberger, 1982 - Atalanta 13:76-77 and by Weidermann, 1982 - Ent. Ztg. 92:159-160.)

Sadly, Blab and Kudrna's recommendations are unlikely to engender the necessary support from the pertinent quarters—major landowners and government agencies. To save Germany's butterfly communities, development must slow down, less land must be converted, more land protected, and old fields laid fallow. All this must evolve quickly in the face of growing German population and a burgeoning economy, in a country with a long history of intensive land use and

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strong tradition of husbandry and cultivation. Blab and Kudrna are inarguably correct in all their prescriptions. Translation of these plans into effective policy is yet another matter altogether.

However, not all the conclusions on which the prescriptions are based are correct. For instance, the conclusion that climatic events play an unimportant role in the dynamics of threatened butterfly populations is most assuredly incorrect. Dramatic and direct effects of climate on butterfly population numbers are well established (Ehrlich et al., 1972, 1980; Murphy et al., 1983; Singer and Ehrlich, 1979; and see Birch, 1957 and den Boer, 1981 for other insect examples). This is important since a concomitant to the fragmentation of habitats is, of course, reduction of habitat area and almost always the disproportional loss of certain microhabitat types. And, it is clear that substantial microhabitat diversity is necessary for the long-term survival of many, probably most, invertebrate species of the temperate zone, where climatic changes, from drought to deluge, are yearly occurrences (Wilcox and Murphy, 1985). The proximate culprit in most documented butterfly extinctions (in fragmented habitats with reduced carrying capacities) is the inability of populations to respond to natural climatic vagaries.

This misunderstanding underscores the unfortunate paucity of population data on German butterflies, and is not a significant lapse in the content of this book. If any disappointment surfaces, it is the short English summary. The translation appears to be directly from the German, thus is extremely ponderous, and as such may not reach the substantial solely English-speaking audience as well as it might have. That same audience, in any case, will appreciate the extensive bibliography of comparatively obscure German works on butterflies. And, for pure entertainment, savor the complete list of German butterfly common names. Think *Carterocephalus silvicolus* is a mouthful, try Schwarzfleckiger Golddickkopffalter!!

This book is must reading for those who would seek the German *Euphydryas* or *Parnassius* amidst the multitude of villages, outwardly-fanning fields, and islands of forest monoculture in a country being transformed into a lush, green biological desert. *Hilfsprogramm für Schmetterlinge* chronicles the last days of entire butterfly communities, and as such soon may be a postscript to the butterflies it features. Wir können nur hoffen daß das nicht die Aussicht fur die Zukunft unserer Schmetterlinge ist!

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Butterflies of South America.
D'Abrera, Bernard. Hill House, Victoria, Australia. 1982. Paperbound edition. 256 pp. (Available in United States from BioQuip Products, Inc., P. O. Box 61, Santa Monica, California 90406, at $19.50 plus $3.00 shipping and handling.)

With perhaps 9,000-10,000 butterfly species found in the Neotropics and our low level of taxonomic sophistication for many groups, it is not surprising that few authors have attempted to distill our knowledge of the neotropical fauna into a single book. Godman and Salvin (1879-1901) in *Biologia Centrali-Americana* (3 volumes) and Seitz (1924) in *The American Rhopalocera, Volumes V* (2 volumes) represent early compilations, while most recently, Bernard D'Abrera has commenced to publish a large-format, multi-volume series on *Butterflies of the Neotropical Region.* All these works are illustrated copiously in color, all are quite expensive, and all are far too large and weighty to carry into the field on a collecting trip to Central and South America. The lepidopterist is reduced to waiting until his return to home base to identify many species, and even then, the price range of the major works mentioned prevent most lepidopterists from acquiring copies for personal reference.

Now D'Abrera has admirably solved the problem with the publication of this portable guide book to the butterfly fauna of South America. The book is inexpensive ($19.50), comprehensive (all principal genera and most obscure genera are figured with representative species), and systematically and usefully arranged (the color figures of almost 700 specimens accompany the species accounts, rather than being grouped in separate plates in random order as in some other publications on South American butterflies). It is hard to guess how the author ever managed to publish a full-color book with this many illustrations at a price under $20.00 U.S., but he deserves our gratitude and admiration even on just this point! The second pleasant surprise is the excellent quality of the color illustrations of each specimen. The novice going to the tropics for the first time as well as the well-traveled professional will have no difficulty learning the basic *gestalt* or overall appearance of a host of genera, especially in the better-known families. The diversity of generic appearances in the metalmarks (family Riodinidae) is covered more briefly than the other families of true butterflies, and the skippers (families Hesperiidae and Megathymidae) are omitted from the book. In the case of the riodinids, D'Abrera makes the true point that the higher classification of this family is more uncertain than any other group, and while he illustrates nearly 70 species of the 2,000 or so species of Riodinidae, this is "simply to demonstrate the prodigious variety of the family", and the user cannot expect to identify many members of this family.

The book begins with a very brief section on the biology, adult morphological structure, physiology, and classification of butterflies. It then proceeds through the various families of true butterflies. Each family section starts with a useful summary of diagnostic and general biological characteristics shared by members of that family. Then a series of generic sections follows, each starting with a brief statement on the approximate number of species in that genus and their general ecology and behavior. A variable number of very brief species accounts (including geographic range and comments on sexual differences) is included in each genus section. The color figures of the adults are reproduced life-size. While most of the illustrated genera and species could be used to identify field-collected specimens, highly polymorphic species or those with many diverse subspecies, such as certain *Heliconius*

and ithomiines, have only several forms figured, and specimens of these species could not be expected to be identified to precise names by use of this field guide. An errata sheet is enclosed with the book, correcting several printer's errors, but overall the text is remarkably free of mislabelings or other errors.

The book's utility lies in it being a simple introduction to the classification and general characteristics of the families, genera, and many species of the true butterflies found in the Neotropics. The *Butterflies of South America* is the best such field guide now available to the lepidopterist, and should be in the working library of everyone interested in the butterflies of the tropical Americas. In fact, I have already two copies, one for my office use and one for field use!

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Butterflies of South America.
D'Abrera, Bernard. 1983. Hill House, Victoria, Australia. Price: US $18.50.

Let's begin with what's good about this book. The color reproduction is mostly quite accurate, and the book does fit neatly in the pocket of a safari jacket or a backpack. On the other hand, its coverage is very nearly random, it is clumsily written, and it is full of errors. In other words, given his recent publications, it is more or less what one would expect from Bernard D'Abrera. And that's a pity, because there is a crying need for a *good* book that does what this book promises (and fails) to do.

The author says in the blurb on the back cover that "Species chosen for treatment in this book are either those most often encountered, or they may be simply very beautiful, or they may typify by their shape or markings those characters by which related species and races may be recognized. But whatever the reason, no hard and fast rule exists for the choice of the nearly 700 specimens figured." That is certainly true. Having been burned by reviewers before, the author adopts an even more defensive tone in his Introduction: "Some omissions (which are always howlingly lamented by the nit-pickers) are deliberate." As an example, he cites the Satyrid genus *Calisto*. *Calisto* is mainly an Antillean genus, barely entering the continent, and is unlikely to be missed. Everyone with field experience in South America can draw up a list of taxa that "belong" in this book but aren't there. A few of the ones I missed—and whose omission seems unjustifiable—are *Styx infernalis*, the extremely bizarre montane Riodinid; *Nathalis plauta* (and, given the incredible diversity of the genus *Colias* on the continent, more than one species might have been figured); the group of *Erebia*-like Pronophiline genera from Patagonia—*Cosmosatyrus chilensis* may be the commonest butterfly in the Southern Cone; and the entire tribe Plebeiini, which, though undiverse in South America as compared to the Theclines, does contain some quite distinctive taxa such as *Parachilades*, *Pseudolucia* and *Itylos*. Obviously no 256-page book can cover the whole South American fauna. But D'Abrera, having decided to reproduce all species life-size (except in the few decorative shots-from-life, which are usually enlarged), makes extremely inefficient use of space (for example, see pages 18, 36, 117, 204, 224-225. . .) and frequently figures several quite similar species of the same genus (*Phoebis, Catagramma*), presumably because he likes them, while not doing justice to the incredible diversity of a genus like *Phyciodes*, for example.

One can live with the omissions and the imbalances, but the errors are another matter. Those who studied D'Abrera's coffee-table-size Neotropical Pierid volume are still giggling over his giving the range of *Eucheira socialis* as "Peru." Mercifully, *Eucheira* did not make this book, but lots of other howlers did. Many of these are a straightforward consequence of D'Abrera's methodology, which consists of plowing through the British Museum and picking specimens with more or less decent data. First the photograph is made and then the data are transcribed. I leave the lowland tropical taxa to specialists, who will, I am sure, find them at least as poorly handled as the high-montane and subantarctic ones. Here are some comments, concentrating on the latter group of taxa.

"None of the Pierids is tailed"—cf. *Eurema proterpia* (p. 61), *Mathania agasicles* (p. 55), *Phoebis rurina* (p. 56). *Pseudopieris nehemia* reaches northern Argentina (p. 53). *Eroessa chilensis*, described as "confined to high altitudes in Chile only" (p. 54), occurs at low to moderate elevations only, and extends in western Rio Negro, Argentina. *Colias lesbia*, described as ranging from "Bolivia to Tierra del Fuego" (p. 56), is not resident south of the Rio Negro in Argentina (unless it is considered conspecific with *C. vautieri*, not figured, which it is not). *Hypsochila* (p. 70) ranges from southern Ecuador and northern Argentina to Tierra del Fuego. The various genera in the *Phulia* group are almost certainly valid (p. 70). There is no obvious reason why "observing these little butterflies (*Phulia*) in the wild, let alone capturing specimens, would be beyond the capacity of most naturalists," as one may drive easily or take a bus (or even a train!) to *Phulia* habitat in Peru, Bolivia, far northern Argentina, and northern or central Chile. *Argyrophorus argenteus* (p. 123) is not very "swift flying." and the elevational range given (3000-8000 feet), while accurate, encompasses extremely different habitats in western Patagonia vs. the Chilean Andes and Coast Range. The genus *Euptoieta* (p. 158) includes high-elevation Peruvian taxa. There is no more excuse for sinking *Yramea* in *Argynnis* (p. 158) than for using *Thecla* for all the Neotropical Theclines, which D'Abrera refuses to do (p. 227). *Yramea anna* was sunk as a synonym of *cytheris* by Herrera in 1951 (p. 158). Contrary to the text, it does not occur in the Atacama Desert, only in the jurisdictional unit called Atacama; its northernmost populations are in Coquimbo and are in a subdesert climate tempered by maritime influence. (The range of this species is amazing enough, without exaggerating.) *Cybdelis* reaches northern Argentina (mountains of Tucuman) (amply documented in Hayward, vol. 3, 1964) (p. 184). Likewise *Epiphele* (p. 185). *Actinote* (p. 221) also reaches at least south to Tucuman. And the map of "biogeographic zones" (p. 6) is so poor it lists the Atacama Desert as "Andes". . .

A few words about the writing: it varies from quite acceptable to utterly execrable. For examples of the latter kind, here is a description of the Riodinidae (p. 239): "so extravagantly and outrageously shaped and decorated as to be almost parodies of the whole Order of Lepidoptera, as if the Creator was having some deeply private Divine joke at His own expense." Of *Phulia* we learn that the elevational range is "anything up to 16,000 ft. (5000 m)," presumably starting from sea level? Neotropical Lycaenids, we learn, "come to certain types of flowers such as inflorescences (which are then attended by other insect orders as well) and umbels." I cannot imagine what the stuff between parentheses means, but umbels *are* inflorescences, and inflorescences are flower-clusters or, more specifically, the dispositions of flowers on the growth axis. And there is no "u" in Falkland Islands (p. 158). And so on.

For professionals and many amateurs, D'Abrera's implied sympathy for a creationist world-view, his frequent allusions to the Creator, and his insinuated distrust of the theory of mimicry may not sit well; at times the book reads like early 19th-Century "natural philosophy," which was natural history at the disposition of religion. But that is a minor matter. The basic problem with this book is that, despite all the consultations acknowledged in the Introduction, D'Abrera doesn't know anything about South America *or* its butterflies. How different this book might have been if written by an experienced Latin American Lepidopterist like Gerardo Lamas or Keith Brown! What a pity it will sell fairly well in the absence of what would be a much better book. *How long must we wait for that book to be written?*

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Coevolution.
Futuyma, D. J. & M. Slatkin (eds.), 1983. 555 pp., 110 illustrations; Sinauer Associates Inc., Sunderland, Mass. 01375. Price: $19.75, paperback.

This is probably the best book to appear on coevolution in recent years (others being *Coevolution of Animals and Plants*, L. E. Gilbert & P. H. Raven, eds., 1975, 246 p.; *Interaction and Coevolution*, J. N. Thompson, 1982, 190 p., and *Coevolution*, M. H. Nitecki, ed., 1983, 392 p.), and at a nice price. The Literature Cited section is 73 pages long! Coevolution may be a relatively new term to many Lepidopterists, although it takes in such familiar topics as mutualism, mimicry, coexistence, competition, plant-animal interactions such as pollination, etc. Coevolution was coined by Ehrlich and Raven in their hallmark paper of 1964 for the mutual, reciprocal evolution of butterflies and their larval foodplants. However, the idea of coevolution apparently originated with Darwin and is the interface between evolution and ecology. Contributors to the 19 chapters include systematists, ecologists, geneticists, and paleontologists. The subject matter covers bacteria, plants, insects, mammals, etc.

Chapter 12 is entitled "Coevolution and Mimicry" by Lawrence E. Gilbert and is well-illustrated and clearly written. He emphasizes Meullerian mimicry, where two warningly colored, distasteful butterfly species converge to the same pattern by predator selection, e.g. in *Heliconius*, although Batesian mimicry becomes more analogous to host-parasite situations. Unfortunately, R. C. Punnett's classic book, *Mimicry in Butterflies* (1915), is not cited. Other discussions particularly appropriate to Lepidoptera are Ch. 10, "Evolutionary interactions among herbivorous insects and plants" by Douglas J. Futuyma and Ch. 13, "Coevolution and pollination" by Peter Feinsinger.

The book is far and away the most comprehensive review on coevolution to date. Like cladistics, coevolution is currently one of the fastest-moving topics in biology. Unlike many topics in evolution and ecology, the theoretical discussions are comparatively easy to understand. It is a college-level text; all but one of the contributors hail from universities.

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Notes

Type Locality of *Papilio indra pergamus* (Lepidoptera: Papilionidae)

Papilio indra pergamus was described by Henry Edwards (1874, Proc. Calif. Acad. Sci. (1)5:423-425) from a single male collected by the coleopterist G. R. Crotch "near Santa Barbara, in May, 1873". The holotype, now in the American Museum of Natural History, bears only the data "Sta Barbara", apparently in Edwards' handwriting.

Other than the holotype, no documented specimens of *Papilio indra pergamus* from Santa Barbara County, California, have been found in searches of all the major museum collections of Lepidoptera in the United States, as well as literature and many personal collections. Tyler (1975, *The swallowtail butterflies of North America*, pp. 18, 62) refers to a "colony in the canyon behind the city of Santa Barbara", but this was based on incorrect information (Tyler, pers. comm.). The subspecies is well known from the mountains of Los Angeles, San Bernardino, Riverside, and San Diego Counties (Emmel and Emmel, 1973, Nat. Hist. Mus. Los Angeles Co. Sci. Ser. 26:11). Since the subspecies is not known from Santa Barbara County (and Ventura County, which falls between Santa Barbara County and the known range), it is likely that the stated type locality is incorrect. It is possible that the subspecies occurs on the entomologically almost unexplored high mountains of Santa Barbara County (e.g., Big Pine Mountain); however, due to inaccessibility (even today), it is very unlikely that Crotch collected there.

The collector of the holotype, G. R. Crotch, travelled throughout southern California from mid March to early May 1873 (Smart and Wager, 1977, J. Soc. Bibliogr. Nat. Hist. 8:244-248). Before and after this, he was in San Francisco, where he was in contact with Henry Edwards. He travelled through San Diego, San Bernardino, and Los Angeles until about 25 April when he sailed to Santa Barbara. He was in Santa Barbara at least 29-30 April (letters from Crotch to Henry Edwards and Herman Hagen in archives of American Museum of Natural History and Museum of Comparative Zoology, respectively). "Early in May" he returned to San Francisco (Edwards, 1874, Proc. Calif. Acad. Sci. (1)5:332-334). Since the holotype bears only Edwards' labels, not Crotch's, it could have been mislabelled by Edwards. Santa Barbara and San Bernardino are easily confused, especially if abbreviated "SB". Edwards incorrectly cited other Crotch data as well. Edwards (1877, Pac. Coast Lepid. 24:5) listed another species collected by Crotch in "July" at Santa Barbara; Crotch was in Oregon and British Columbia in July.

Thus, the type locality of *Papilio indra pergamus* is not "near Santa Barbara", but is farther south, probably mountains near San Bernardino. To avoid further confusion, I fix the type locality of *pergamus* to Devil Canyon, about 11 km NNW of San Bernardino, San Bernardino Mountains, San Bernardino County, California, a well known locality for the subspecies (Emmel, pers. comm.).

I thank F. M. Brown, J. F. Emmel, R. C. Priestaf, F. H. Rindge, H. A. Tyler, and the curators of the collections and archives consulted, for assistance and information.

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Six Homoeotic *Vanessa atalanta rubria* (**Nymphalidae**)

Six homoeotic individuals of *Vanessa atalanta rubria* (Fruhstorfer) eclosed from 6-19 July 1982 in the third generation of a culture established 19 February 1982 from larvae collected at Barlow Canyon, Ventury County, California. They represent what is only suspected to be the third inbred generation, since the wild P_1 larvae were probably offspring of unrelated females. The F_1 adults which were paired were most likely sibs because a variant phenotype, informally referred to as "brunnea" in the culture, occurred in 15 out of ca. 150 F_2 sibs. Two pairs of these F_2 "brunnea" adults were mated, producing over 800 ova. The majority of the resulting F_3 were "brunnea" phenotypes, ca. one-fourth were similar to typical *V. a. rubria*, and six of these more typical phenotypes were homoeotic (Figs. 1-6). They are most likely siblings.
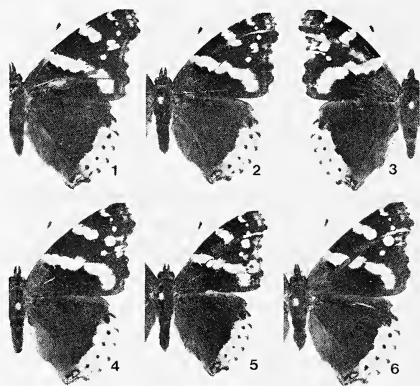
Figs. 1-6. Homoeotic *Vanessa atalanta rubria*. Sex and dates of emergence (all 1982): **Fig. 1,** male, 6 July; **Fig. 2,** female, 6 July; **Fig. 3,** male, 9 July; **Fig. 4,** female, 9 July; **Fig. 5,** male, 12 July; **Fig. 6,** female, 19 July.

The homoeotic areas involve the right forewings of five of the specimens and the left forewing of one. Only the upper surface of each wing is affected except in two specimens where a small area of wing and scale deformity has caused an unpigmented spot. Three specimens are males, three are females.

Sibatani (1983, A Compilation of Data on Wing Homoeosis in Lepidoptera. J. Res. Lepid. 22:1-46, 118-125) has recently reviewed all known cases of homoeotic Rhopalocera. He notes a lack of reports of homoeotic specimens from America, so the specimens reported here will correct this situation. Homoeosis has been recorded only once before in this species (Sibatani, *loc. cit.*), but this is for the European subspecies *V. a. atalanta* (L.).

Shapiro (1981(83), Two Homoeotic *Pieris rapae* of Mexican Origin (Pieridae). J. Res. Lepid. 20:242-244) has reported two homoeotic *Pieris rapae* (L.) that are most likely sibs, and Gardner (1963, Genetic and Environmental Variation in *Pieris brassicae*. J. Res. Lepid.; 2:127-136) reports rearing three homoeotic specimens from one brood of over 300 *Pieris brassicae* (L.). The addition of the six homoeotic *V. a. rubria* reported here would seem to support the genetic predisposition presumed by Shapiro (*loc. cit.*) to occur in some inbred cultures.

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INSTRUCTIONS TO AUTHORS

Manuscript Format: Two copies *must* be submitted (xeroxed or carbon papered), double-spaced, typed, on 8½ x 11 inch paper with wide margins. Number all pages consecutively and put author's name at top right corner of each page. If your typewriter does not have italic type, underline all words where italics are intended. Footnotes, although discouraged, must be typed on a separate sheet. Do not hyphenate words at the right margin. All **measurements** must be metric, with the exception of altitudes and distances which should include metric equivalents in parenthesis. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as example: 4. IV. 1979 (day-arabic numberal; month-Roman numeral; year-arabic numeral). Numerals must be used before measurements (5mm) or otherwise up to number ten e.g. (nine butterflies, 12 moths).

Title Page: All papers must have the title , author's name, author's address, and any titular reference and institutional approval reference, all on a separate title page. A **family citation must** be given in parenthesis (Lepidoptera: Hesperiidae) for referencing.

Abstracts and Short Papers: All papers exceeding two typed pages must be accompanied by an abstract of no more than 300 words. An additional summary is not required.

Name Citations and Systematic Works: The first mention of any organism should include the full scientific name with author (not abbreviated) and year of description. New descriptions should conform to the format: male: female, type data, diagnosis, distribution, discussion. There **must** be conformity to the current International Code of Zoological Nomenclature. We strongly urge deposition of types in major museums, all type depositions must be cited.

References: All citations in the text must be alphabetically listed under Literature Cited in the format given in recent issues. Abbrevations must conform to the *World List of Scientific Periodicals.* Do not underline periodicals. If four or less references are cited, please cite in body of text not in Literature Cited.

Tables: Tables should be minimized. Where used, they should be formulated to a size which will reduce to 4 x 6½ inches. Each table should be prepared as a line drawing or typed with heading and explanation on top and footnotes below. Number with Arabic numerals. Both horizontal and vertical rules may be indicated. Complex tables may be reproduced from typescript.

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COVER ILLUSTRATION: *Euphydryas editha* in copula (Almont Summit, Gunnison Co., Colorado). Worn male above and teneral female below. See Ehrlich & Wheye, page 143.

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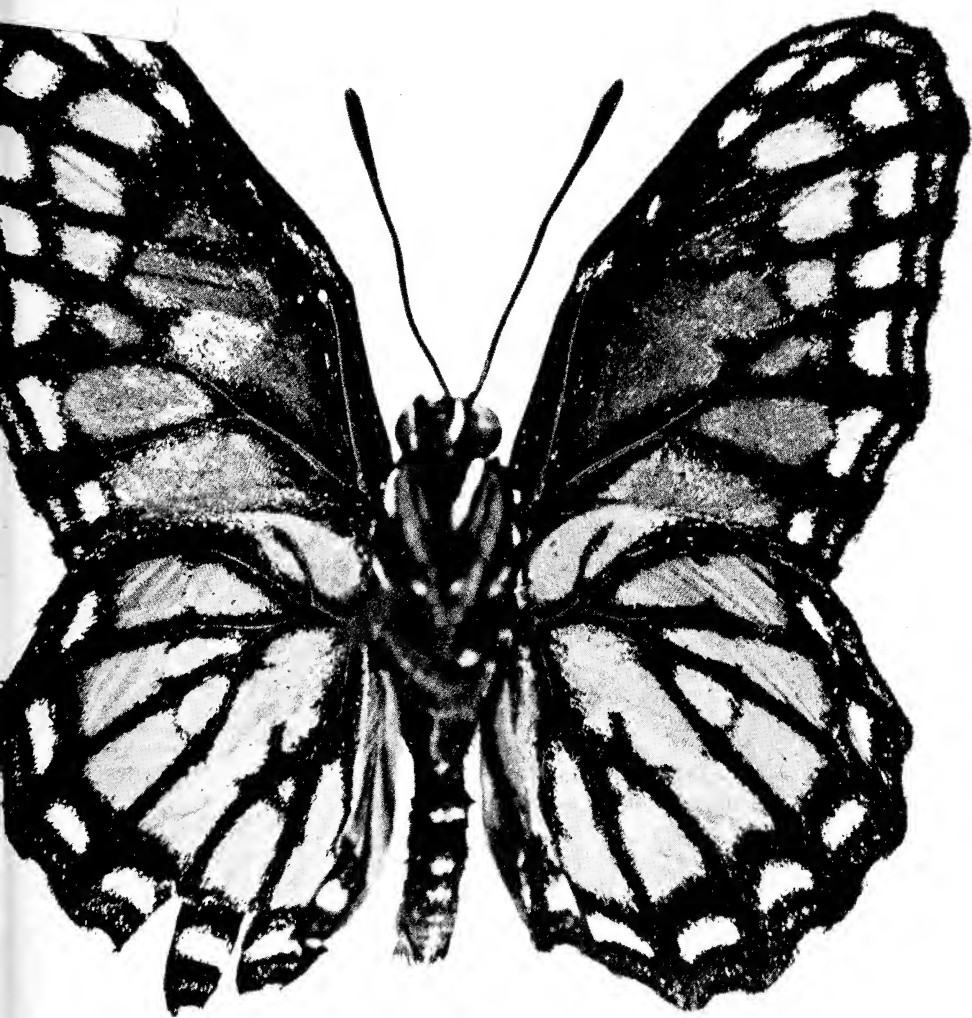
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Invited Paper

Polyphenism, Phyletic Evolution, and the Structure of the Pierid Genome

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Abstract. Pierid polyphenism is discussed in the context of various contemporary issues in evolutionary biology. It is concluded that: 1. Geographic variation in the physiological control of polyphenisms represents adaptive "fine tuning" via classic microevolutionary processes. 2. The overall control of the epigenetic processes of polyphenism, as analyzed in hybridization studies, demonstrates a simple genetic architecture compatible with microevolutionary processes. 3. Phenotypic differentiation among species and among seasonal phenotypes within species does not support paleontological models linking speciation to morphological change and "genetic revolutions." 4. Concealed phenotypic plasticity is useful for inferring evolutionary history. 5. Genetic aberrations and purported atavisms may also be useful, but must be interpreted cautiously. 6. Phenotypic plasticity may contribute to stabilizing the genome, sheltering it from directional selection and thereby contributing to the perplexing phenomenon of long-term evolutionary stasis.

Introduction

. . .whoever compares the discussions in this volume with those published twenty years ago on any branch of Natural History, will see how wide and rich a field for study has been opened up through the principle of Evolution; and such fields, without the light shed on them by this principle, would for long or for ever have remained barren.

> Charles Darwin, in his "Prefatory Note" to the English edition of *Studies in the Theory of Descent* by August Weismann, 1882.

Charles Darwin died in 1882, the same year the English edition of Weismann's *Studies in the Theory of Descent* appeared. Weismann's book is very largely about Lepidoptera, and especially about the plasticity of their phenotypes. There is no record that Darwin himself experimented in this area, perhaps because so many of his illustrious contemporaries—on both sides of the Atlantic—were already doing so. Weismann attributes the first such experiments to Dorfmeister (1864). They thus have a history of over 120 years, all of it after the publication of *On the*

Origin of Species, and represent an important and recurrent theme in evolutionary biology. Butterfly experiments were central to the theoretical development of two of the most original and distinctive minds in the history of evolutionary biology, Weismann himself and Richard Goldschmidt. They were also critically important in the debate between Darwinians and neo-Lamarckians early in this century. Between the 1860s and World War II butterfly polyphenisms were frequently discussed in connection with almost all the scientific issues in biology. Since then, however, they have lain largely neglected while evolutionists had radically different things on their minds. Yet today the issues of greatest interest in evolutionary journals are ones familiar in the writings of both Weismann and Goldschmidt; indeed both men have been "rediscovered" and are cited with greater frequency today than for decades. This implies that butterfly polyphenisms are "relevant" to mainstream evolutionary biology again. I propose that they are, and in this paper I propose to discuss what messages they may hold for evolutionists in general.

How Polyphenism Has Been Studied

Polyphenism is the production of two or more phenotypes in individuals which do not differ in their genetic makeup. We may contrast it with polymorphism, in which by convention the phenotypes reflect underlying genetic (usually allelic) differences. (This is not the strict sense of "polymorphism" as used in the population-genetics literature, where it refers to allelic frequencies at a locus, but is a "looser" sense which comes closer to the original organismal point of reference.) Polyphenism is thus by definition an *epigenetic* phenomenon, that is, it concerns the processes whereby the genetic information is translated into a phenotype. But it is also a *genetic* phenomenon insofar as in some sense the program of translation is itself encoded in the genome, as it must be, since different species—even closely related ones—are not equipotent in this regard. This is exactly the focus of the growing discipline of developmental genetics, which tries to understand the nature of epigenetic processes, and which had its roots in the Lepidopteran studies of Goldschmidt and Kühn. There is considerable diversity of opinion today as concerns whether, or to what degree, epigenetics is an epiphenomenon of the genome. We shall return to this.

Historically, polyphenism in butterflies has been studied mostly in a proximate—mechanistic—organismic physiological manner. Let us recall briefly the very useful causal analysis of adaptation presented by Mayr (1961). Any adaptation may be studied at both *proximate* and ultimate levels of causality. Proximate here refers to the mechanisms (developmental, physiological, behavioral, etc.) whereby the adaptation is realized in the individual. Ultimate causality includes both the genetic basis for the proximate mechanisms and the ecological factors, which—serving as agents of natural selection—led to the fixation of the genes in

question. There is no innate superiority in one approach as against the other; commonly they are reciprocally illuminating, as in the present case.

There is a fashion current in the evolutionary literature of distinguishing studies of "process" from those of "pattern" (Eldredge and Cracraft, 1980). This is a revival of a 19th-century tradition (Coleman, 1971). Developmental biology, epigenetics and the physiology of phenotypic determination by environmental factors are all matters of "process." But polyphenism can also be studied as "pattern." For example, one may deal literally with pattern—the relationships among pattern elements among alternate phenotypes may, for example, be studied using classical comparative methods (Shapiro, 1984a). Other "pattern" studies may seek to correlate phenotypes with seasonal, climatic and geographic factors; such correlative studies in turn enable us to construct and test hypotheses concerning function, thereby returning us to studies of "process," and comprehension of phenotypic norms of reaction permits us to predict things about seasonal and geographic patterns. And so on.

"Pattern" studies commonly are structured inductively. Thus, if we find the same geographic pattern of phenotypic variation recurring in different phyletic lineages in the same environments, we are led to infer common causality and to ask what it might be. Of course, we must be able to recognize different lineages when we see them. It is easy to say that the virtually congruent seasonal polyphenisms of *Araschnia levana* and *Pieris napi (sensu lato)* must be convergent because one is a Nymphalid and the other a Pierid; the likelihood that both got the system from a shared proximate ancestor is very remote. It is much more difficult to decide whether the seasonal polyphenisms of the *callidice* and *napi* species-groups of *Pieris* in the Holarctic are homologous, and whether either or both is homologous with the polyphenisms of the *Tatochila sterodice* species-group (also pierine) in the southern cone of South America. But it is theoretically possible and certainly worth trying.

The moral of this section is that understanding the evolution of polyphenism involves us in phylogenetic inference, whether we are systematists or not.

Mechanisms and "Fine Tuning"

Temperature does not act on the physical constitution of the individual in the same manner as acid or alkali upon litmus paper. . .rather. . .climate, when it influences in a similar manner many succeeding generations, gradually produces such a change in the physical constitution of the species that this manifests itself by their colors and markings.

> A. Weismann, *On The Seasonal Dimorphism of Butterflies* (Trans. R. Meldola, 1882)

An overview of mechanisms (proximate causation) for butterfly polyphenisms is given in Shapiro (1976a). In general, seasonal polyphenisms are under some combination of photoperiodic and temperature control in temperate latitudes. In tropical latitudes photoperiodic information is often of little value, and control is probably mostly related to temperature and humidity variations, Other factors, such as food quality and crowding, are relevant in specific cases.

Photoperiod is also of little value in some mid-latitude environments. One would predict on Darwinian grounds that temperature would predominate in phenotypic control in such environments, and this seems to be the case. For example, Hoffmann (1978) showed that Rocky Mountain *Colias philodice eriphyle* are essentially refractory to photoperiod, and depend on temperature, in the control of ventral hindwing melanization. (They are, however, sensitive to photoperiod in diapause induction.) This would be expected if melanization is thermoregulatory in function, since the daily regime of insolation (afternoon cloudiness) is essentially invariant over the entire flight season. Shapiro (1977a) found the same thing in coastal Californian *Pieris napi venosa*; in some years summer may actually be colder than spring due to advected fog associated with the cold California Current. Short-term prediction, based on temperature autocorrelation, is more valuable in such regimes than the longer-term seasonal prediction derived from photoperiodic information.

In the same vein, Shapiro (1978a) presented a schematic representation of the developmental options available to *Pieris napi (sensu lato)*. It seems likely that all of them have been realized in one or another population, though not all exist in any single one.

Shapiro (1978a, 1982) also showed that it is the *rule*, rather than the exception, for multivoltine polyphenic species to have multiple systems of phenotypic determination, with a hierarchy of precedence which can be rationalized adaptively. Thus, normally, short-day (long-night) phenotypic determination is irreversible by subsequent experience: a mild autumn does not imply winter is not coming. (On the other hand, warm conditions usually shorten the critical photoperiod for diapause induction, a form of reproductive gambling.) But long-day (short-night) regimes do not really "determine" phenotype—subsequent chilling will produce the hibernal phenotype. Implicit in this observation is the assumption that photoperiods do not lie, that winter is a long way off, but that means must be found to get through the present spell of adverse (cold) weather. It is scarcely surprising that phenotypes in Rocky Mountain *Pieris napi macdunnoughii*, sympatric with Hoffmann's *Colias*, are under a mixture of genetic and temperature control, with no photoperiodic influence. Photoperiod is more important in eastern *P. n. oleracea* (Oliver, 1970); in its range flight seasons are longer and there is more temporal variation in climate to deal with. Populations of the *napi* group from extreme northeastern California (Modoc County) are seemingly closely related to *macdunnoughii* but have quite distinct

seasonal phenotypes with a probable photoperiodic component.

Such sorts of variation in the control of polyphenism strongly imply adaptive value and even adaptive "fine tuning" to environment. Such "fine tuning" is becoming well-documented in life-history studies (Denno and Dingle, 1981) and is the classic stuff of microevolution. In insects it is particularly well-studied as regards diapause (Dingle, 1978; Brown and Hodek, 1983).

Local adaptation, however, is not universal. In part this may be due to "phylogenetic inertia," a theme to which we shall return shortly. In part, however, the exceptions may be useful in making the rule more comprehensible. An outstanding case is the Western White, *Pieris occidentalis*.

This very abundant species seems to have a very low degree of local differentiation with respect to phenotypic determination, despite occurring from high plains to above timberline, with one to three or more broods per year. Indeed, the exceedingly dark "*calyce*" phenotypes found above tree-line in the Rockies, which have been suspected of being a different species, produce normal *occidentalis* when reared in appropriate conditions, and all *occidentalis* populations studied so far appear able to produce *calyce* in the lab, whether or not it occurs locally in nature (Shapiro, 1974a, 1975, 1976b). One explanation of the invariance is extensive gene flow, and this is a widely dispersing species (Shapiro, 1977b) whose "hilltopping" behavior would be expected to promote vertical genetic mixing, preventing the differentiation of a true alpine ecotype (Shields, 1967; Shapiro, 1974a). Presumably this would also be reflected in a low degree of differentiation at electrophoretic loci, an hypothesis we are currently testing.

Montane *Colias eurytheme* which co-occur with *C. p. eriphyle* retain their photoperiodic sensitivity, failing to parallel the seasonal biology of the other species. But *eurytheme* is only a temporary seasonal invader in these habitats, re-establishing itself by immigration every year—so local adaptation should not be expected, at least not in the short term. (This is similar to the situation in *Nathalis iole*, Douglas and Grula, 1978. In both cases phenotype is keyed to photoperiod but there is no diapause, and both species are highly vagile and largely fugitive.) Many common butterflies, especially in the western United States, are "weedy," and it is doubtful whether local populations last long enough to be considered meaningful units of evolution. Rather, they are expressions of a vast "metapopulation" (Gill, 1978) in which local adaptation is unlikely (cf. Shapiro, 1974b re *Plebeius acmon*). *Pieris rapae* has a population structure of this sort, as shown electrophoretically, but it shows clines in physiological adaptation (Vawter and Brussard, 1984; F. Slansky, pers. comm.; Shapiro, unpubl. data).

How Polyphenisms Evolve

When we are able to change many specimens of the summer brood into the winter form by means of cold, this can only

depend upon reversion to the original, or ancestral, form, which reversion appears to be most readily produced by cold—that is, by the same external influences as those to which the original form was exposed during a long period of time, and the continuance of which has preserved, in the winter generations, the color and marking of the original form down to the present time.

A. Weismann (*Ibid.*)

Polyphenisms, like diapause, appear to evolve in response to local conditions by the selective adjustment of proximate physiological mechanisms. In other words, what evolves is the "setting" of the threshold which changes the developmental instructions from phenotype 1 to phenotype 2. Microevolutionary fine tuning of this sort can be studied by hybridizing populations, races, subspecies, or species which differ in their thresholds, then working out the genetic control of the differences. The usual assumption made in such studies is that the character in question will be polygenic (i.e., best described not by simple single-locus Mendelian segregation but by the models of quantitative genetics). Because individual variation in response to environment is intrinsic in such systems (a fact of great interest, because it implies a genetic "risk-spreading" strategy in which selection perpetuates a certain level of "error" in response to environmental uncertainty; the validity of this hypothesis remains to be explored), their analysis can only be statistical in character. Studies of this sort have yet to be reported for butterfly phenotypes, though we have several in progress. They are handicapped by the fact that whole genomes, not just specific loci related to wing patterns, are mixed at hybridization; unknown developmental or genetic incompatibilities may be introduced, such that one cannot be sure that preimaginal mortality is random with respect to prospective phenotypes. Thus one cannot be sure inadvertent selection has not taken place, unless the broods are large enough for sophisticated treatment. Also, nearly all studies of incompatibility in butterfly hybrids, including various Pierid papers, are open to question because of the small numbers of replicates and the failure of the authors to report levels of incompatibility in control crosses *within* populations. Lorkovic (1978 and pers. comm.) is cognizant of the problem, but also of the practical problems in properly controlling such studies.

It is somewhat easier to study the genetic control of polyphenism in crosses between entities which are polyphenic and others which are not. To date this has been achieved only for the South American *Tatochila sterodice* species-group; it is exceedingly desirable that it be repeated for say, *Araschnia levana* X one of its monophenic Asiatic congeners. The *Tatochila* studies are still in progress, but have been reported in part in Shapiro (1984b, 1985). The "genetic architecture" of polyphenism is proving to be quite simple, involving one major locus and a variable, but thus far always small, number of modifiers. Parsons (1983) reviews the

literature of the genetic basis of supposed quantitative traits, including developmental (epigenetic) ones, and finds "an underlying genetic architecture of a few genes of relatively large effect. . . .even if a trait has an outwardly continuous distribution." In other words, our results are surprising only when compared to the standard assumptions which, overall, are falsified by a large accumulation of data from a variety of organisms and traits. We shall return to this theme also, in the context of the tempo and mode of transspecific evolution.

The Relation Between Phenotype and Speciation

It should be evident that the large literature of the genetics of species differences in outbreeding animals (Ayala, 1980, 1982) gives no comfort to advocates of simplistic general models. Nonetheless, contemporary evolutionary biologists find themselves in an ongoing controversy pitting so-called "phyletic gradualism" against "punctuated equilibrium" as the "primary" mode of transspecific evolution. The latter position, generally attributed to Eldredge and Gould (1972), grew out of the observation by paleontologists that the fossil record seems to imply very long periods of morphological "stasis" ("equilibrium") within lineages, "punctuated" by abrupt speciation events. Paleontologists generally (for want of better) base new taxa on morphological change. (Neontologists do too, but to the extent that live animals can be procured and reared, they can test their inferences against the "biological species concept;" this is how we know, for example, that *Pieris occidentalis* and *"calyce"* are conspecific. One cannot do genetic experiments with dead animals.) There is thus an inevitable circularity in how paleontologists think about "speciation;" for them sibling species are beyond the pale of knowability. The consequence was a generalization that has led to all sorts of trouble: that "speciation" is essentially "instantaneous" and accompanied by profound morphologic change (which is interpreted as reflecting profound *genomic* change).

The problems with this view have been addressed extensively (Charlesworth, et al., 1982; Stebbins and Ayala, 1981, etc.). It is necessary, however, to point out that no one familiar with butterfly polyphenisms could accept this paleontological generalization. Seasonal phenotypes of butterflies are often much more different than are congeneric species whose reproductive isolation is nearly or quite complete. *Pieris napi napi* and *P. balcana* are nearly identical phenotypically, but reproductively isolated (Lorkovic, 1978). *P. n. nesis* and *P. n. japonica* are partially overlapping in Japan; they are phenotypically differentiated and rarely hybridize in nature, but are capable of doing so (Suzuki, et al., 1979). Each, however, resembles the corresponding seasonal form of the other more than it resembles its own alternate seasonal form (cf. plates in Eitschberger, 1983). The extremely complex group of *"napi"* entities on the Pacific Coast of North America is at least equally enigmatic, with seasonal polyphenism within taxa seemingly evolving more rapidly than phenotypic divergence among them (Shapiro, unpubl. data). A pre-

liminary electrophoretic survey suggests that phenotype is more divergent in *P. protodice* and *P. occidentalis* than is the structural genome. There are no hard-and-fast rules here.

The simple genetic architecture of polyphenism in the Andean *Tatochila sterodice* species-group is mirrored in the genetics of wing-pattern differences among taxa, just as in the large literature of hybridization in the Papilios (Robinson, 1971). We have studied the inheritance of some two dozen color and pattern characters in a very extensive program of hybridization, including nearly all the possible crosses among five of the six taxa in the group, often carried to the F_3 or F_4. We have also studied the genetics of genitalic characters which have been alleged to be species-specific (Herrera and Field, 1959)—the third time the genetics of a genitalic character have been worked out, and the second time in a Lepidopteran (Shapiro and Porter, in prep.). Nearly all the taxonomically significant differences among the taxa are simply controlled and for the greater part unlinked. This includes the genes controlling sexual dimorphism, which varies greatly in the group, seemingly in a manner correlated with climate. Platt (1984) summarized generally similar results from his very extensive hybridization program in the genus *Limenitis* (Nymphalidae). Here, however, reproductive incompatibility is pronounced in certain crosses. The most incompatible combinations all involve *L. arthemis*, whose mimetic pattern is the most divergent in the genus. However, Platt presents a good argument for the incompatibility arising secondarily in sympatry, rather than being due to the loci involved in the pattern divergence *per se*: incompatibility is an inverse function of geographic distance. Given that the traditional model of reinforcement of reproductive isolating mechanisms is today under attack (e.g. Paterson, 1978), this is an especially interesting observation. (In *Tatochila* there are no barriers to quantitate against distance.) One hopes to see further analysis of compatibility data from Platt's crosses (Platt, et al., 1978; Platt, 1984).

There is a widespread belief that speciation itself is not an adaptive process, at least insofar as it occurs by differentiation of populations in allopatry. (Secondary reinforcement may be viewed as adaptive insofar as it "protects" coevolved gene complexes from disruption via hybridization, but it occurs in secondary sympatry.) The differentiation of seasonal phenotypes is inferred to be an adaptive process because of the convergences and parallel environmental and geographic gradients noted above. To date only one seasonal polyphenism, that of *Colias eurytheme*, has been shown to be adaptive by a demonstration of function (Watt, 1968, 1969); even here the actual fitness advantage has not been quantitated in the field, but the conclusions are inescapable. it is, of course, not formally possible to prove that polyphenism was originally selected for by thermoregulatory needs, even if it were shown that it is maintained by such selection today. Shapiro (1976a) showed in a small-scale survivorship study that the polyphenism of *Pieris occidentalis* was potentially adaptive to weather, but the mechanism was not explored. Roland (1982) found that ventral hindwing melanization in the univoltine *Colias*

nastes and *Colias meadii* was correlated with levels of flight activity.

If the functional advantage of the vast majority of polyphenisms remains obscure, it is in part due to the complexity of polyphenic variation itself. Seasonal phenotypes consist of many characters, which have more or less freedom to vary independently of one another. Kingsolver (1985) discusses some of the constraints from an engineering standpoint. We may eventually be able to apply such reasoning to construct robust tests of "optimal adaptation" hypotheses in butterfly wing patterns. In the meantime, the overall character of seasonal variation does make sense, which is encouraging. *Pieris* and *Colias* have smaller wings relative to body size, and less produced wing apices, in cold-season broods. The same features are found in arctic and alpine pierines and coliadines. Anyone who has observed the behavior of these animals should realize the significance of these features. Vernal, arctic, and alpine animals fly low and very deliberately, within their "boundary layer," exercising a great deal of control over their own movements and avoiding if at all possible rising into the usually active air flow above the "boundary". Estival—and tropical lowland—animals usually fly higher, routinely leave their boundary layer, and often rise with thermals, more or less passively. Our experiments to date indicate that the wing shapes of both arctic-alpine and tropical species are pretty tightly canalized, so that rearing under bizarre conditions produces little modification (though it is often in the right direction). Thus one can see both the raw material on which selection can act in adapting either cold- or hot-climate butterflies to a regime of alternating hot and cold seasons, and vice versa. The mechanisms for such selection are in the literature (Waddington, 1961).

I have pointed out elsewhere (Shapiro, 1984a) that the highly derivative estival phenotype of the male *Tatochila vanvolxemii*, from the seasonal temperate mid-part of Argentina, is a reinvention of *Ascia*—whatever it might be "good for." *T. vanvolxemii* is partly sympatric with *A. monuste*, which is a migratory species in Argentina. One of the most astonishing aspects of the convergence is that the male *vanvolxemii* has two genetic forms of discal dot: one is smaller than the normal *Tatochila* spot and looks like the spot on *Ascia (Ascia)*; the other is larger than in other *Tatochila*—and looks like the condition in the other subgenus of *Ascia, Ganyra*!

To sum up: in the adaptive sense, the phenotypic differences within polyphenic species do not seem qualitatively different from those which characterize genetic species. The same selective pressures may apply, and only a few loci need be involved. There is no simple mapping of phenotype on genotypic differentiation in butterflies.

Phylogenetic Inference

If this hypothesis is correct—if the variety *bryoniae* is really the original form preserved from the glacial period in certain regions of the earth, whilst *napi* in its winter form is the first secondary form gradually produced through a warm climate, then it would

be impossible ever to breed the ordinary form *napi* from pupae
of *bryoniae* by the action of warmth, since the form of the
species now predominant must have come into existence only be
a cumulative action exerted on numerous generations, and not
per saltum. . . .Experiment. . . .confirmed (this)view.

A. Weismann (*ibid.*)

Inferring phylogeny from concealed variation is a technique which has
been rediscovered almost as often as penicillin. It is, basically, merely an
extrapolation of the normal pattern of phylogenetic inference, which has
been so integral a part of biological education for 125 or more years that
the repeated rediscovery of its implications is not at all surprising. The
logical structure of Basile's (1969) inferences concerning the evolutionary
history of morphology in liverwort gametophytes is identical to that of
Shapiro's (1971) work on the patrimony of *Pieris virginiensis*. Due to the
very different literatures in which these papers appeared (and the lack of
"key words" in their titles), neither author was aware of the other until
1981 when Shapiro happened to see a reference to Basile's paper in a
symposium on (!) vicariance biogeography. In response to an inquiry,
Basile wrote (Sept. 15, 1981): "It is clear that our separate attempts to
understand mechanisms underlying phylogeny have led to the same
generalizations—that derived taxa have not necessarily lost morpho-
genetic capacities, and much can be learned about evolution by
experimental procedures which 'free' latent or suppressed developmental
processes." This approach is developed in detail by Shapiro (1981), with
examples. With reference to Pieridae, it is combined with classical com-
parative methods to reconstruct pattern evolution (Shapiro, 1984a).

All such studies of necessity require assumptions. The first and
foremost is that the direction of evolutionary change (the "polarity of
morphoclines or transformation series" in cladistic jargon) can reason-
ably be inferred. Hennig's famous rules for this are nothing but an explicit
statement of conventional (evolutionary, pre-cladistic) "common sense,"
but they are useful. It *is* reasonable, for example, to infer that it is easier to
lose (suppress) a phenotypic character than to gain one, and that charac-
ter states associated with specific ecological situations have a high proba-
bility of arising more than once in a lineage. In the case of pierine
polyphenisms these statements, taken together, imply that the full ven-
tral pattern is the primitive condition and the more or less immaculate
estival pattern is derivative from it, and likely to have arisen more than
once. This precise logic was used by Weismann in his analysis of the *napi*
group over a century ago, and subsequently by Kautz (1955). Both these
authors and Shapiro (1984a) agree on the direction of pattern evolution,
though in 1882 Weismann was "on the fence" about innate physiological
propensity as against natural selection, and Kautz was an explicit

orthogeneticist. Anyone who retains any doubts about parallelism in the evolution of seasonal polyphenisms in the *napi* group should look at the summer forms of various taxa illustrated in color by Eitschberger (1983) Though Eitschberger is more of a classical morphotaxonomist than an evolutionist, his data unambiguously point to parallelism rather than direct homology in the loss of pattern in summer forms.

The problems of inferring parallelism and convergence from studies of the physiology and developmental biology of polyphenism have been discussed by Shapiro (1980, 1981). They are likely to remain until specific genes responsible for the phenomena have been identified and sequenced; this will be a long wait, given the poor state of Lepidopteran cytotechnology. In the meantime we can test hypotheses generated from such studies by looking for other, independent indicators of affinity. In our lab, phylogenetic reconstruction by cluster analysis of electrophoretic—genetic data has borne out the inference that the Holarctic pierines and the south American *Tatochila* evolved seasonal polyphenism convergently. There is also a suggestion that polyphenism probably evolved independently in *Pieris (Artogeia)* and *P. (Pontia, Pontieuchloia, Synchloe)* (Geiger and Shapiro, unpubl. data). Ordinary genetic studies of hybrids of the two polyphenic *Tatochila, mercedis* and *vanvolxemii*, have also borne out the hypothesis that they evolved polyphenism separately (Shapiro, unpubl. data). Unfortunately, not all searches for taxonomic congruence are so successful.

This discussion has dealt with characters "around the species level," that is, microevolution. The logic used by Basile and Shapiro has been used, however, to reconstruct phylogeny at much higher levels. Thus, Hampé (1959) experimentally restored the ankle articulation of *Archaeopteryx* in the chicken, and Kollar and Fisher (1980) convincingly demonstrated the presence of latent genes for tooth enamel synthesis in the same much-put-upon bird. All such studies are, however, haunted by the specter of Slijper's goat (Slijper, 1942a,b). (This is one of the most famous case histories in functional morphology. Born without forelegs, the animal adopted a bipedal gait and underwent a clearly adaptive series of skeleto-muscular changes paralleling those found strongly canalized in normally bipedal species. Could this imply latent ancestral bipedalism in goats? — The question is only ludicrous because one thinks one knows the patrimony of goats.) Nonetheless, it is striking, and probably significant, that the equatorial Andean pierines are not latently polyphenic (Shapiro, 1977c, 1978b). Nor is *Pieris sisymbrii* in the Nearctic, and it is not only the only obligately univoltine Nearctic pierine, it is also, electrophoretically, a very primitive *Pontia*, far back in the Holarctic dendrogram and very possibly antedating the origin of polyphenism in its sublineage.

The regularity with which interspecific pattern evolution (as in the *Tatochila sterodice* group) parallels intraspecific (polyphenic) evolution,

permitting phylogenetic inference in both cases, with neither the assumption of homology nor of any "genetic revolution," underscores once again the dangers of simple generalizations about transspecific evolution. We will learn more by studying the genetics of epigenetic control in crosses of sister-species such as *Pontia daplidice* and *P. glauconome*, which differ in this regard. Alas, they first must be interfertile.

Atavism and Pattern Evolution

There are many claims of atavism (reversion) in the butterfly literature. Many of them are probably valid, but the probability of actually establishing their genetic basis is poor—and nearly all the aberrations end up on pins rather than in breeding cages. "Atavism" is a mixed concept, incorporating both back or reverse mutation and other sorts of genetic events which are of more evolutionary interest; most of this discussion will concern one such case.

The frequency of claims of reversion should give pause to those few systematists who continue to adhere to a rigid version of Dollo's "law"—the "irreversibility" of evolution. Character reversals appear to occur with great abandon in the Pieridae; not just the formalisms required for resolving contradictions in cladistics, but the real thing.

The aberration *"funebris"* appeared spontaneously in a cross of hybrid origin in the *napi* group (Lorković, 1971). Its basic effect is to convert the *Pieris* pattern to something resembling a *Colias* pattern above. Kautz (1955), by inference only from the *napi* group, and Shapiro (1984a), from pierines in general, postulated a primitive pattern of two dark lines parallel to the outer margin of the wings, and it is easy to visualize these as in turn derivative from a broad, solid coliadine-type border. Bowden (1983) interpreted *"funebris"* as a "paleomorph," analogous to the uncovering of a latent ancestral condition as described above. The actual pattern of melanization, however, does not fully support this idea. The discal spots, which are universally interpreted as the remains of the inner of the two lines, lie beyond the solid border and are fused to it on their outer edges, which is to say *"funebris"* fills in the area *between* the lines but does not reverse the suppression of the portions of the inner line which are normally missing. Since hybridization between coliadines and pierines is impossible, and no living pierine appears to produce a primitive coliadine pattern as wild type, the question of whether or not *"funebris"* is atavistic is unlikely to be resolved. However, some interesting and suggestive things can still be learned about it.

Bowden (*loc. cit.*), following Riedl (1978), interprets the genetics of *"funebris"* in the context of its hybrid origin. Riedl argues that hybridization can liberate concealed ancestral phenotypes by disrupting the gene-complexes which normally suppress their expression. In *Drosophila*, Thompson and Woodruff (1980) find that crosses of widely separated

geographic strains show elevated mutation rates, and attribute this to disruption of gene-complexes which suppress mutation (or enhance repair) within populations. The precise genetic nature of *"funebris"* has thus far eluded analysis. If *"funebris"* were ancestral to all wild-type *napi* patterns, this implies that different suppressor systems would have evolved in different populations or, in effect, that the modern *napi* pattern is polyphyletic. This is best studied by putting *"funebris"* into a variety of *napi* populations, which we are doing.[1]

Such changes of genetic context, requiring successive backcrossing, also are useful in demonstrating the extent to which the expression of *"funebris"* is subject to control by the polyphenic-epigenetic system. Within the initial genetic context, the degree of susceptibility to such control seems quite limited (Bowden, 1983 and *in litt.*). If the Bowden-Riedl interpretation were correct, would we expect *"funebris"* to circumvent such control or to be subject to it? This depends on whether the liberation of the latent phenotype entails the total inactivation of its suppressors, because these would presumably have evolved in coadaptation with the polyphenic system. The stock in which Bowden has maintained *"funebris"* is relatively weakly polyphenic; its performance in the very strongly polyphenic Nearctic *napi* will be of great interest. Whatever it tells us about atavism, it already has helped to define the developmental fields for pierine wing patterns and to test the models of Kautz and Shapiro for their evolution.

Where Does Evolutionary Stasis Come From?

. . .this. . .is equivalent to the statement that every species through its physical constitution, is impressed with certain fixed powers of variation, which are evidently extraordinarily numerous in the case of each species, but are not unlimited; they permit of a wide range for the action of natural selection, but they also limit its functions, since they certainly restrain the course of development. . .in this directive influence lies the precise reason why. . .from a given starting-point, the development of a particular species cannot now attain, even under the most favorable external conditions, any desired goal; and why, from this starting-point, given courses of development. . .must be restricted, just as a ball rolling down a hill is directed by a fixed obstacle in a direction determined by the position of the

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[1]Kautz reasoned as if *napi* could be treated in a vacuum or at least as if the *napi* complex were primitive in the Pierini. The dorsal pattern of the *napi* complex (which is most affected by *funebris*) is shared with the *rapae* group, the *brassicae* group, and with *krueperi*, whose relationships remain unclear. The preliminary electrophoretic evidence (H.-J. Geiger, pers. comm.) does not support any such generalization. In the Andean genus *Hypsochila* it appears that a *"rapae*-pattern" has evolved from a *"napi-*(or *callidice-*) pattern," but the direction of pattern evolution in the Holarctic pierines is much more open to question.

latter, and depending on the direction of motion and the
velocity at the moment of being diverted.

> A. Weismann (*ibid.*)

Macroevolution turns out to be reducible to microevolutionary
processes. Or at least, the theory of punctuated equilibria can-
not serve as an argument for the decoupling of macroevolution
from microevolution. Consequently, however, there is no reason
to expect that the mechanisms of the origin of evolutionary
novelties are within the reach of paleobiological analysis. The
research program intended to analyze macroevolutionary change
should focus first of all upon relationships of canalization and
plasticity to various ecological regimes. . .to reconcile evolu-
tionary ecology and developmental biology. Perhaps this can be
done within the conceptual framework of the neo-Darwinian
synthetic theory.

> Antoni Hoffman, in Grene (1983), p. 262.

Stasis is a real evolutionary phenomenon, not only at the morphological
level as perceived by paleontologists, but at the molecular level too.
Explaining it is a major unresolved problem for evolutionary biology. Van
Valen (1982) reviewed the phenomenon and identified 11 possible
mechanisms, of which six can be reduced to the three most-often-cited
explanations: gene flow, stabilizing selection, and developmental con-
straints ("phylogenetic inertia"). (The others are too restrictive or
improbable to be taken seriously as *general* explanations.) There are
strong empirical and theoretical objections to both of the first two, and
the third is poorly understood. We cannot hope to resolve the matter here,
but some comments on the Pierid genome and the notion of "phylogenetic
inertia" may be useful.

Developmental constraints were initially advocated by Eldredge and
Gould (1972) as the most probable cause of stasis. Such "constraints,"
however, can be of various kinds; the most esthetically satisfying one, and
the one apparently on Eldredge and Gould's minds, is that the timing of
developmental events is so critical to successful ontogeny that anything
which would tend to alter it is likely to be lethal (or if not, to produce a
cascade of events leading to major phenotypic change, a macromuta-
tion). This is pure Goldschmidt; it should not be forgotten that his ideas,
expressed to a wide audience in his 1938 book, came about equally from
work on the developmental and physiological genetics of *Drosophila* and
of Nymphalid wing patterns. The butterfly work has been largely forgot-
ten, in part because it was published in German in pre-war Germany, in
part because the cytotechnology never improved, and in part because it
was tainted with Lamarckism.

The usual rejoinder of pro-selectionists to the "inertia" argument is

that many characters have been selected radically by man, with rapid directional response and no sign of developmental disequilibrium resulting (cf. Charlesworth and Lande, 1982, also Falconer, 1960 and Lewontin, 1974). An alternative explanation is that some parts of the genome are readily selectable ("open") and others are not ("closed") (Carson, 1973, and various papers by A. Templeton).

This problem cannot be considered apart from the concept of developmental canalization (Waddington, 1957; Rendel, 1968). This concept, and even its name, recall Weismann's metaphor of the rolling ball on the incline. In an ecological context, developmental flexibility provides an economical alternative to genetic polymorphism as a response to a variable environment. If the environment is, moreover, *predictable*, phenotypic switching becomes the optimal response, doing away with both genetic load (except for "risk-spreading" or "bed-hedging" strategies, noted earlier) and the lag time of selective response. Epigenetic arrangements which allow for adaptive phenotypic plasticity, such as butterfly seasonal polyphenisms, would tend to stabilize substantial portions of the genome by doing away with seasonally-related selection; not only seasonally sensitive loci would be affected, though, since linkage groups could be tightened and the internal integration of the genome enhanced overall. To the extent that epigenetics is an epiphenomenon of the genome (rather than an emergent system property inherent in cells but independent of specific loci), it should be selectable. In the case of diapause and of polyphenism, it certainly appears to have been selected.

Pattern polyphenisms, as we have seen, may involve multiple and profound phenotypic changes (morphological, behavioral, and probably biochemical), which imply that blocks of genes are under common control mechanisms, perhaps in a manner akin to the "supergenes" of polymorphic mimics (Robinson, 1971) or the X-linked "sex package" of *Colias* (Grula and Taylor, 1980a,b), but probably not, as the phenotypic components are freer to vary among themselves. Whatever the physiology, the alternative to viewing these facts in an adaptive light is to fall back on Slijper's goat.

The suggestion is that neither developmental constraints nor stabilizing selection alone accounts for most stasis. Instead, what we may be seeing is directional selection acting on the genetic control of epigenesis, generating a system of plasticity which in turn generates its own stabilizing selection. This is the basic notion at the heart of H. G. Baker's "general purpose genotype" (1965). It is a rather different notion from Lerner's (1954) "genetic homeostasis," which is essentially an extrapolation of the idea of overdominance or hybrid vigor, but the two converge insofar as phenotypic plasticity is in a sense a form of permanent heterozygosis. (This is the reverse of genetic assimilation.)

Most such feedback processes will result in things more subtle than

wing pattern polyphenisms, and may go unappreciated. Giesel *et al.* (1982) published a cautionary tale on life-history traits in *Drosophila*, noting that heritabilities and genetic correlations may behave differently in different environments. The remarkable paper of James, 1983, on the environmental component of morphological variation in birds is highly relevant, too. The idea that evolved phenotypic plasticity is a general enough phenomenon to warrant consideration as a major factor in stasis is *not* far-fetched. Indeed, it can be found in Wright (1931), one of the great papers of population genetics.

By being as conspicuous as they are, polyphenic butterflies—especially pierines—have reminded us that the organism is not necessarily a passive receiver of environmental buffeting on the tortuous road to extinction. By genomic reorganization it can potentially opt out of directional selection, at least for some things. Adaptation is potentially a two-way process.

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A Review of *Polygonia progne (oreas)* and *P. gracilis (zephyrus)* (Nymphalidae), including a new Subspecies from the Southern Rocky Mountains

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Abstract. *P. progne* and its subspecies *oreas* and *silenus* have differently-shaped gnathos and tegumen, and have blacker undersides of their wings, than have *P. gracilis* and its subspecies *zephyrus*. A new subspecies of *P. progne* is described from the Southern Rockies, characterized by the underside and abdomen structures of *progne* and *oreas*, the upperside of *P. gracilis zephyrus*. The new subspecies is uncommon and has only one generation, versus two in *zephyrus*. Larvae of *P. progne* subspecies eat gooseberry, rarely currant, whereas larvae of *P. gracilis* subspecies eat currant. An interesting convergence is shown to affect the wing pattern in many species of *Polygonia* and one species of *Asterocampa*, which deserves further study. A synopsis of Nearctic *Polygonia* is given.

Introduction

Brown et al. (1957) correctly listed the presence of *P. progne* (as *P. silenus*) in Colorado, illustrating a female and describing a male which represent the subspecies described herein (both are figured in the present Figs. 1-2). Brown was somewhat doubtful about their identity, and all other authors writing on the southern Rockies fauna have assumed that Colorado-Utah-Wyoming-southern Montana *progne* or *oreas* are just dark variants of *P. zephyrus*. Thus Ferris et al. (1981) illustrated the underside of the *P. progne* subspecies described below, yet treated it as a "brown form" of *zephyrus*. The present paper documents the presence of this new Southern Rockies subspecies of *progne*, resembling *progne* and *oreas* on the underside, and *zephyrus* on the upperside. The paper clarifies the confusion that has surrounded *Polygonia progne, oreas, gracilis,* and *zephyrus*. For instance C. dos Passos and P. Ehrlich (in Ehrlich and Ehrlich, 1961) combine *P. oreas* and *zephyrus* into one species, and treat *progne* and *gracilis* as distinct species. The wing pattern intergradation between *P. gracilis* and *P. gracilis zephyrus* led me to investigate the species ranges and morphology.
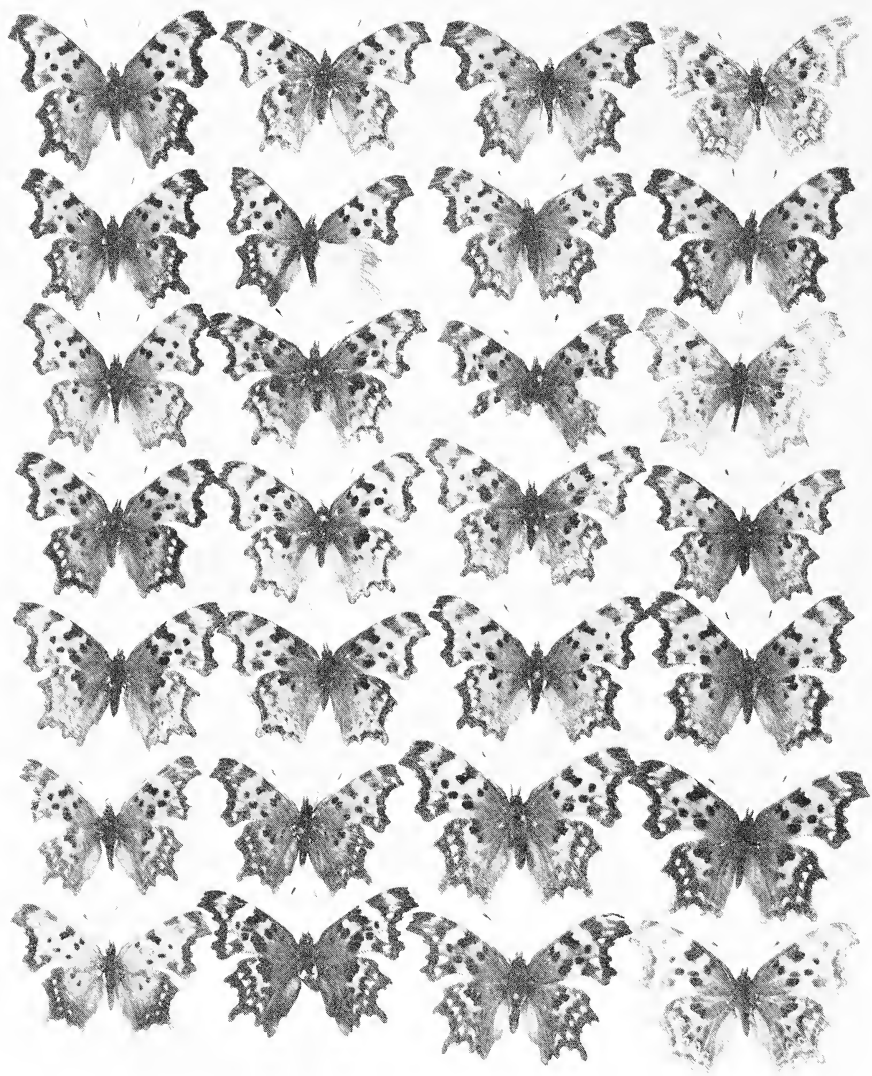
Figure 1
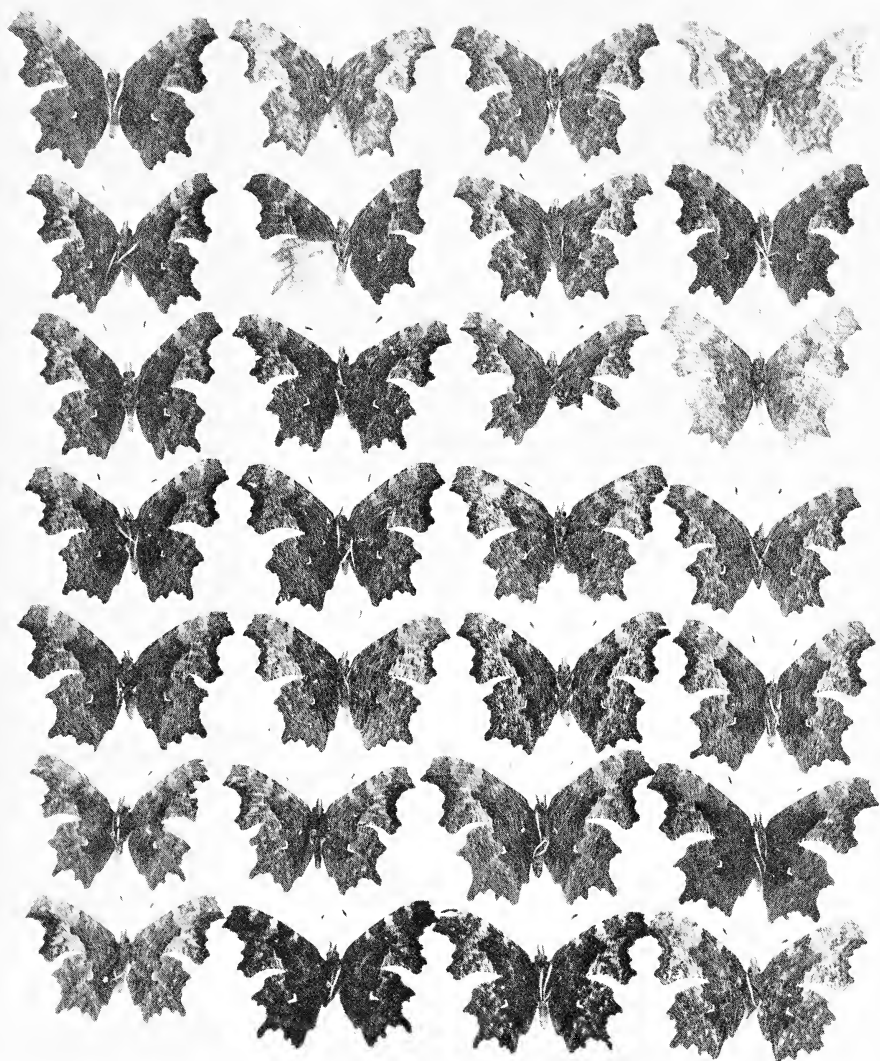
Figure 2

Fig. 1.   Rows 1-5 are types of *nigrozephyrus* (paratypes unless stated, in the
collection of the collector unless stated otherwise). **First Row** males:
Gregory Cany., 6200′, Boulder Co. Colo. 4 Aug. 67 Ray E. Stanford
(RES); Woodmen Valley, 7000′, El Paso Co. Colo. 10 July 77 James A.
Scott (JAS); Gregory Can. 1 May 66 JAS; Williams Canyon, 7400′, El
Paso Co. Colo. 11 Aug. 71 JAS; **Second Row** males: Indian Creek
Campgound, 7300′, Douglas Co. Colo. 16 Aug. 69 RES; Cheyenne Mtn.,
9400′, El Paso Co. Colo. 5 Aug. 31 F. Martin Brown (FMB) in Univ. Colo.
museum (CU), (right hw scales rubbed off many years ago to study
venation), this male discussed by Brown et al. 1957, who list its altitude
as 9000′; Lump Gulch near Rollinsville, 8500′, Gilpin Co. Colo. 7 Sept. 28
Hugo Rodeck, holotype, in CU museum; Indian Creek Campground 16
Aug. 67 RES; **Third Row** males: Flagstaff Mtn., 6900′, Boulder Co.
Colo. 1 June 73 RES; Wild Cherry Creek, 8700′, Sangre de Cristo Mts.,
Saguache Co. Colo. 16 Aug. 74 JAS; Twin Lakes, 9500′, Lake Co. Colo.
18 Aug. 52 FMB, in CU museum (abdomen missing); Bruce's Spruce
Camp, 9000′, San Juan River, [Mineral Co.] Colo. 27 May 39 FMB, in CU
museum; **Fourth Row** females: Williams Can. 11 Aug. 71 JAS; stream
at NW edge of Minturn, 7900′, Eagle Co. Colo. 22 Aug. 69 JAS; Wild
Cherry Creek 29 May 72 JAS; Flagstaff Mtn. 14 April 65 JAS; **Fifth Row**
females: Bavarian Lodge, 8500′, Aspen, Pitkin Co. Colo. 18 Aug. 37
FMB, allotype, in CU museum, figured as "silenus" by Brown et. al. 1957;
Woodmen Valley 19 July 75 Michael Fisher, in JAS coll.; near Deckers,
6400′, Douglas Co. Colo. 18 May 69 RES; Indian Creek Campground 12
Aug. 72 RES; **Sixth Row:** Tilden Regional Park, Contra Costa Co. Calif.
13 April 68 male *oreas*, Paul A. Opler; Halfmoon Park, Crazy Mts.,
Sweetgrass Co. Mont. 16 Aug. 66 male *oreas*, JAS; same, female; Miller
Creek, Missoula Co., Mont. 15 Sept. 83 female near *oreas*, Steven J.
Kohler; **Seventh Row:** Minneapolis, Minn. 25 Aug. 65, female *progne*;
Cameron Lake, S. Vancouver Isd., B.C. 6 Aug. 51 male *silenus*, Richard
Guppy (RG), in CU museum; Errington, Vancouver Isd., B.C. 18 April 52
male *silenus*, RG, in CU museum; Wellington, S. Vancouver Isd., B.C. 8
Aug. 51 female *silenus*, RG, in CU museum.

Fig. 2.   Undersides of adults in Fig. 1, in same positions.

Genitalic Characters

I found that both *P. gracilis* and its subspecies *zephyrus* have a longer
and thinner gnathos and a slightly more rectangular anterior margin of
the tegumen, whereas *P. progne* and its subspecies *oreas, silenus,* and the
new subspecies have a much shorter, wider, more elbowed gnathos and a
slightly more rounded tegumen (Figs. 3-4). The two species are very dif-
ferent in structure, and no hybrids between *P. gracilis* and *P. progne* have
been found. Brushing the abdomen tip of males (and sometimes removing
the abdominal shell above the genitalia) exposes the genitalia sufficiently
for identification (and brushing the tip is usually required even to deter-
mine the sex, because wing shape and abdomen volume are unreliable for

sex determination). The only intraspecies variation found is in the valva of male *P. progne progne*, which often has a smaller dorsal notch, but this trait is too variable for use in identification. Female genitalia did not prove useful for identification.

Polygonia progne

Using these male genitalic traits, I examined all of the available adults having a blackish-gray underside, and found every male to be genitalically *progne*, not *gracilis zephyrus*. The Southern Rockies *progne* were found to be a new subspecies, described as follows:

Polygonia progne nigrozephyrus J. Scott, new subspecies

The subspecies is characterized by a dark (blackish-gray, not "brown") underside as in subspecies *progne* and *oreas*, and a dorsal hindwing resembling *P. g. zephyrus* in having very large yellow submarginal spots (Table 1). All the known adults have large submarginal yellow spots on dorsal hindwing as in *zephyrus*, except a male from Cheyenne Mountain (Fig. 1) which is somewhat similar to subspecies *progne*. Black dorsal spots vary greatly in size in *nigrozephyrus* (Fig. 1). *P. p. nigrozephyrus* differs from *P. g. zephyrus* in the generally darker underside (some adults are fairly similar), the male genitalia, the single brood, and in hostplants (Table 2). Subspecies *nigrozephyrus* has one yearly generation in Colorado (emerging late July and August, overwintering, then flying, mating, and laying eggs through May) as have *oreas* and *silenus* in the rest of the west (except two generations occur in lowland California *oreas*), whereas *P. g. zephyrus* has two generations at least at low altitude in Colorado (late June-early August, then September overwintering to May; Scott and Scott, 1980). *P. progne progne* has two generations except in northern Canada; *P. g. gracilis* has one generation. The new subspecies occurs from 5800-9500 feet (1800-2900 m) altitude, in Transition and Canadian Zones, in habitats with fairly open forest of pines (Ponderosa or Lodgepole, sometimes also Pinyon) and sometimes Douglas fir and Aspen, and various shrubs (even oak), the habitats dry to fairly moist.

The name *nigrozephyrus* is assigned because most persons have assumed that the adults are merely "dark *zephyrus*".

There are 29 types (19 male, 10 female). All were examined, including the genitalia of all males except the one paratype with abdomen missing. Holotype male Lump Gulch, Gilpin Co., Colo., 7 Sept. 1928, Hugo Rodeck, in University of Colorado museum. The holotype, allotype, and. most paratypes are figured in Figs. 1-2 and their localities and repositories listed in the legends. The remaining paratypes are: Sugar Creek near Deckers, 7500-8000', Douglas Co., Colorado, 16 Aug. 1970, 1 paratype male, Mike Fisher (in M. Fisher collection); foot of Lookout

Polygonia progne   **Polygonia gracilis**
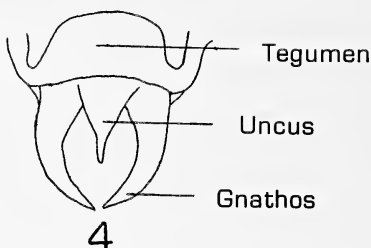
Figs. 3 & 4. Dorsal view of male genitalia of *P. progne (oreas, silenus, nigro-zephyrus similar) and P. gracilis (and zephyrus).*

Mountain, 6100', Golden, Jefferson Co., Colorado, 25 March 1972, 1 paratype female, Donald E. Bowman (J. Scott collection); Surface Creek, 8 miles northeast of Cedaredge, Delta Co., Colorado, 7500', Richard L. Klopshinske, 28 Aug. 1983, 1 male, 1 female paratypes in RLK collection, 3 male paratypes in J. Scott collection, 1 Sept. 1983, 1 male paratype in J. Scott collection; West Creek, 9 miles northeast Gateway, Unaweep Canyon, Mesa Co., Colorado, 5800', 11 Sept. 1983, R. L. Klopshinske, 1 paratype male in RLK collection.

Additional localities for *P. p. nigrozephyrus* are: Lambs Canyon Branch of Parleys Canyon, east of Salt Lake City, 7000', Salt Lake Co., Utah, 28 Aug. 1898, 1 male, G. Wesley Browning (genitalia borrowed and examined; wings typical of *nigrozephyrus* with large yellow dorsal hind-wing submarginal spots, Clyde F. Gillette written communication); west slope Sierra Madre Mountains, Carbon Co., Wyoming, 18 July 1977, C. Ferris (underside figured by Ferris and Brown eds. 1981, but upperside and genitalia not seen). In addition, a female from City Creek Canyon, Salt Lake Co., Utah, 25 Aug. 1929, Dr. John W. Sugden, was not seen but is described as *nigrozephyrus* by C. Gillette. *P. p. nigrozephyrus* seems limited to mountainous Colorado, Utah, southern Wyoming, and probably northern New Mexico.

The ranges of other *P. progne* subspecies in the Rocky Mountains were clarified somewhat. Adults from Converse County Wyoming ("several specimens from Converse Co. were determined as *progne* by C. F. dos Passos", Ferris, 1971) and Bighorn Mountains Wyoming (*"progne"*, Macy and Shepard, 1941) probably are *P. p. progne*, or perhaps are *P. p. progne-oreas* intermediate populations. *P. p. oreas* (type locality California, Brown, 1967; hereby restricted to Contra Costa Co.) occurs from central coastal California (Monterey, San Francisco, Alameda, Contra Costa, Marin, Sonoma Cos.) and northern California (Plumas and Sis-

Table 1. Differences between *P. progne* and *gracilis* subspecies. UPF, dorsal forewing; UPH, dorsal hindwing; UNH, ventral hindwing.

	silenus	*oreas*	*nigrozephyrus*	*progne*	*zephyrus*	*gracilis*
Wing Shape	slightly more ragged than *oreas*	normal	normal	normal, but fw sometimes more produced	normal, but fw sometimes more produced	normal
Size of median black UPF spots beyond discal cell	very large cell CuA_2; large cell CuA_1; absent or large cell M_3	large (rarely small) CuA_2; small to large CuA_1 (rarely just trace)	large to small CuA_2; absent to large CuA_1	very small or small in cell CuA_2	small (rarely large) CuA_2; absent or trace CuA_1	small (rarely very small or large) in CuA_2; sometimes a trace or small CuA_1
Size of other black UPF and UPH spots	very large	usually large	variable, large to small	very small, sometimes small	small	small
Submarginal yellow spots in brown UPH border	small, rarely large	small, rarely large or very small	large, often very large, rarely small	very small	large, often very large, rarely small	very small, sometimes small
Width of brown UPH border	normal	normal	normal	normal (winter), half wing width (summer), usually blended	normal	normal, sometimes wider and blended into orange
Color of wing undersides	nearly black male, blackish-gray female, russet edge & lines	blackish-gray	blackish-gray	blackish-gray	gray, rarely nearly blackish-gray	blackish-gray, but postmedian area whitish
UNH lower arm silvery comma	long (2 mm)	long, sometimes very short	usually short, sometimes long or absent	absent, sometimes moderate or long	moderate (rarely absent or long)	moderate
Thorax color ventrally	blackish male, blackish-gray female	dark gray	gray (sometimes dark gray)	gray (sometimes dark gray)	gray	gray
Leg color (tibia and tarsus)	white	whitish-gray	whitish-gray to gray	gray (rarely whitish-gray)	gray or whitish-gray	whitish-gray

Table 2.   Hostplants of *Polygonia progne* and *P. gracilis*[17]

Polygonia progne	Polygonia gracilis
progne	**gracilis**
Ribes (Grossularia) rotundifolium Michx.[1] (Grossulariaceae)	*Ribes (Ribes) triste* Pallas[10]
R. (Grossularia) missouriense Nutt.[2]	*R. (Ribes) glandulosum* Graver[10]
R. (Grossularia) "wild gooseberry"[3]	*Ribes* "wild currant"[11]
Ribes "currant"[4]	
Rhododendron nudiflorum (L.) Torr.[5] (Ericaceae)	**zephyrus**
Betula papyrifera Marsh.[6] (Betulaceae)	
	Ribes (Ribes) cereum Dougl.[12]
oreas	*R. (Grossularioides) montigenum* McClatchie[13]
	R. (Grossularioides) lacustre (Pers.) Poir[14]
Ribes (Grossularia) divaricatum Dougl.[7]	*Ribes* "wild currant"[15]
Ribes species with spiny fruits and stems (not *divaricatum*)[8]	*Menziesia glabella* (Gray) Calder & Taylor[14] (Ericaceae)
	Rhododendron occidentale (Torr. & Gray) Gray[16] (Ericaceae)
silenus	
Ribes (Grossularia) divaricatum[9]	

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17 H. Tietz (1972, An Index to the Described Life Histories, Early Stages and Hosts of the Macrolepidoptera of U.S. and Canada, Allyn Museum) lists other hosts, which seem to be errors so are not listed.

kiyou Cos.) northward to Oregon-Washington and southeastern British
Columbia east of the Cascades, east to Idaho, Montana, and northern
Wyoming. New county records since those mapped by Ferris and Brown
eds. (1981) are: Teton Co., Wyoming (probable, based on "American
Museum Natural History records", Ferris, 1971); Chouteau Co., Mon-
tana (McMurtry Creek, Highwood Mountains, 14 Aug. 1966, 1 male, J. A.
Scott; Highwood Mountains, 7 Aug. 1963, one female in University of
Colorado museum whose dorsal hindwing resembles subspecies *progne*
somewhat); Cascade Co., Montana, Harley Creek, Little Belt Moun-
tains, 15 Aug. 1966, 2 males, J. Scott; Gallatin Co., Montana (T.
Valente); Aldridge and Park Counties, Montana (Thomas Rogers);
Mineral, Glacier, Ravalli, Deer Lodge, and Beaverhead Counties, Mon-
tana (Steven Kohler); Fremont Co., Idaho (Jon Shepard); Boise Co.,
Idaho (Manning and Nelson Curtis); Idaho Co., Idaho (record from Ray
Stanford). *P. p. silenus* (type locality Portland, Oregon, Brown, 1967)
seems limited to the Cascade Mountains from southwestern British
Columbia to Oregon and possibly California (intermediate to *oreas* in
coastal Mendocino Co., John Emmel, written communication). North-
western Montana *P. progne* near *oreas* are most similar to *oreas* (the
sexes are similar for instance), but are somewhat darker than California
and central Montana *oreas* on the underside, indicating that some
intergradation with *silenus* occurs from there west to southeastern
British Columbia-eastern Washington and perhaps into eastern Oregon.
True Cascades *silenus* are strikingly distinct, as noted in Table 1 and
Figs. 1-2; adults near *oreas* are paler east of the Cascades including in
eastern Washington (Jon Pelham, written communication). In central
Montana, some *oreas* adults are somewhat similar to *progne* (the dorsal
hindwing yellow submarginal spots and dorsal forewing median black
spot in cell CuA_1 "Cu_1" often small), presumably reflecting introgression
from *progne* to the north and east. *P. p. progne* has recently been found in
Rosebud Co., Montana (Ray Stanford).

I treat *oreas* as a subspecies of *progne* because they share identical
genitalia, underside, larval pattern details (though the ground color of
progne larvae differs somewhat and varies greatly), and gooseberry
(*Ribes*) larval hostplants, and are barely allopatric, their ranges adjacent.
P. p. progne extends northward from where *oreas* and *silenus* stop in
southern British Columbia and extreme southwestern Alberta (*progne*
occurs in central British Columbia and the Alberta plains northward to
the Northwest Territories of Canada, east to eastern North America).
The range of *progne* does not make ecological sense by itself, because it
extends from Arkansas and North Carolina to the Northwest Territories,
yet is absent from western U.S., where *oreas, silenus,* and *nigrozephyrus*
replace it, existing over a greater range of rainfall (nearly 500 cm per year
near Seattle, to 40 cm near Denver) than *progne*. *P. p. progne* does look

different from western *oreas* and *silenus*, but of course so also does *nigrozephyrus*, which heretofore was lumped into another species (*zephyrus*). The winter generation of *progne* lacks the broadly-black dorsal hindwing margin of summer generation *progne*. This leaves the size of the yellow submarginal dorsal hindwing spots and the size of the dorsal forewing median black spot in cell CuA_1 as the major differences between *progne* and *oreas*, characters which vary, especially in *oreas* (both characters) and *nigrozephyrus* (the latter character mainly, Fig. 1). It must be emphasized that *oreas* is intermediate between *progne* and *nigrozephyrus* in the former character, and intermediate between *progne* and *silenus* in the latter character. The relationship between *progne* and *oreas-silenus* may perhaps be clarified by further sampling where their ranges extend near each other, and noting whether the wing pattern intergrades; unfortunately *oreas* and *silenus* are uncommon, and large series do not exist. It should be noted that, until corroborated, the *P. silenus* record of Gibson (1920) from the Klotassin River area, Yukon, may be mislabeled, because *silenus* is otherwise unknown north of southern British Columbia, and *progne* is unknown from the Yukon as well. The specimen, an apparent female in the Canadian National Collection, is correctly identified, based on slides sent by J. Donald Lafontaine. Possibly *silenus* extends along the coast of British Columbia (where *progne* is absent) to Yukon, but proof is required.

Polygonia gracilis

P. gracilis gracilis and *P. g. zephyrus* are clearly subspecies. They intergrade broadly from Manitoba to Alaska (J. Donald Lafontaine notes this in adults in the Canadian National Collection, written communication), many series from Yukon for instance have variants resembling both subspecies and intermediates, and even southward to northern Washington and northern Montana some *gracilis* tendencies appear occasionally (the underside more two-toned). In Alberta, adults from Banff to Jasper in the mountains are usually intermediate (Norbert Kondla, written communication). See Table 1 for distinguishing characters.

Convergence and Competition between Species

Species of *Polygonia* show amazing examples of parallel variation (convergence). Form "umbrosa", in which the outer half of the dorsal hindwing is black, occurs in summer-generation adults of *Polygonia interrogationis, P. comma,* and *P. progne progne* in eastern North America, and eastern *P. gracilis gracilis* sometimes have a wider black margin as well. *Astercampa clyton* (Boisduval and LeConte) also has a black dorsal hindwing form in northeastern U.S., but not on the Gulf Coast or Arizona. Surely this "umbrosa" convergence is one of the major

puzzles about eastern U.S. butterflies, yet it has received almost no attention. The convergence explains why *P. p. progne* diverged in appearance away from *P. p. oreas*. In western North America, in contrast, both *P. progne nigrozephyrus* and *P. gracilis zephyrus* are pale on the same area of the wing (as is *P. satyrus*, which is widespread and common in western North America but limited in range and uncommon in eastern North America). Doubtfully mimicry, the convergences perhaps result from virus-transferred genes??

A related phenomenon may be the comparative abundance of the *Ribes*-feeding *Polygonia*. In eastern North America *P. gracilis gracilis* is usually uncommon, and *P. progne progne* is usually fairly common, whereas in western North America *P. gracilis* (and *zephyrus*) is usually common, and *P. progne (oreas, silenus, nigrozephyrus)* is nearly always uncommon to rare. The reason for this is not known; it doubtfully involves competition for larval food, which is generally common.

The available evidence further suggests there is no competition for larval food because larvae of *P. progne* prefer gooseberry, whereas *P. gracilis* larvae feed on currant (Table 2). "Gooseberry" (*Grossularia* Mill.) is a subgenus (a separate genus in Abrams, 1944) of *Ribes* L. which differs from "currants" in the flowers and stems. In *Grossularia* the pedicels are not jointed beneath the ovary (jointed in currants), the stems have spines at the nodes, and the calyx tube is always more than 2 mm long above the ovary (it varies in length in subgenus *Ribes*). Several currant species (*R. lacustre* (Pers.) Poir and *R. montigenum* McClatchie) do have spines on the twigs, but these have the calyx tube shorter than 2 mm; they are sometimes separated as the subgenus *Grossularioides* Jancz., the remaining spineless currants being subgenus *Ribes*. Noting in the table that all the *Ribes* hostplants of *P. progne* that are identified to species are gooseberries, *Grossularia*, one can conclude that *P. progne* (including *oreas* and *silenus*) larvae prefer gooseberry. In contrast, numerous records indicate that larvae of *P. gracilis* (including *zephyrus*) eat only currant. The next question to ask is: does the abundance of gooseberries versus currants in the various regions of North America have anything to do with the abundance of *P. progne* and *P. gracilis* subspecies? I cannot answer this question for all of North America, but there may be some correlation in Colorado, where *nigrozephyrus* is very rare west of Denver northward to Wyoming in the Front Range, where Wax Currant *Ribes cereum* is by far the commonest *Ribes*, but is slightly more numerous (uncommon) in Douglas and El Paso Counties and west of the continental divide, where gooseberry is common.

Adults of *P. progne* and *P. gracilis* feed on tree sap, rotten fruit, mud, and nectar of various flowers. *P. p. nigrozephyrus* adults fed on yellow *Chrysothamnus nauseosus* flowers in the fall (R. Klopshinske).

Synopsis

The following summarizes the names involved, including all other Nearctic *Polygonia*. Note that form names no longer are subject to the rules of nomenclature so that forms "umbrosa" and "silvius" are also applied to the same forms in species and subspecies other than those in which the forms were originally named, much as the names of genetic forms such as the A, B, and O blood groups are applied to chimpanzees as well as humans. The concept of *hylas* and *rusticus* has been changed to correspond with the wing pattern and hostplant variation within *P. faunus*. *P. comma* and *P. satyrus* have similar undersides, but are sympatric in Manitoba, Ontario, Quebec, New Brunswick, Nova Scotia, Minnesota, Wisconsin, Michigan, and Maine, without known intermediates, though they may occur. Note the spelling of *interrogationis, neomarsyas,* and *c-argenteum*. The biological and morphological reasons for this arrangement are given further by Scott (1985).

P. interrogationis (Fabricius) 1798
   = *fabricii* (W. H. Edwards) 1870 (winter adult)
   Summer form *umbrosa* (Lintner) 1869
     = *crameri* (Scudder) 1870
P. comma (Harris) 1842
   = *harrisii* (W. H. Edwards) 1873 (winter adult)
   Summer form *umbrosa* (same form as in *P. interrogationis*)
     = *dryas* (W. H. Edwards) 1870 (summer adult)
P. satyrus (W. H. Edwards) 1869
   = *chrysoptera* (W. G. Wright) 1905
   = *neomarsyas* dos Passos 1969
   = *hollandi* Gunder 1927
P. progne (Cramer) 1776 TL New York
  a. *progne*
    = *c-argenteum* (W. Kirby) 1837 TL 54°N, Cumberland House Saskatchewan (winter adult)
    = *martineae* Coleman 1919 TL probably Connecticut
    Summer form *umbrosa* (same form as in *P. interrogationis*)
      = *l-argenteum* Scudder 1875 no TL (summer adult)
  b. *oreas* (W. H. Edwards) 1869 TL Contra Costa Co., California
  c. *silenus* (W. H. Edwards) 1870 TL Portland, Multnomah Co., Oregon
  d. *nigrozephyrus* J. A. Scott 1984 TL Lump Gulch, Gilpin Co., Colorado, holotype University of Colorado museum
P. gracilis (Grote & Robinson) 1867 TL Mt. Washington N.H.
  a. *gracilis*
  b. *zephyrus* (W. H. Edwards) 1870 TL Virginia City, Storey Co., Nevada

P. faunus (W. H. Edwards) 1862 TL Hunter, Greene Co., New York
a. *smythi* A. H. Clark 1937 TL Mt. Rogers, Grayson Co., Virginia
b. *faunus*
c. *hylas* (W. H. Edwards) 1872 TL Berthoud Pass, Clear Creek Co., Colorado (Saskatchewan-Alaska-Colorado-Oregon, small in size, underside gray, hostplants *Salix, Ribes,* etc.)
   = *arcticus* Leussler 1935 TL Black Mountain, near Aklavik, Northwest Territories
   Unspotted underside female form *silvius* (same form as in *rusticus*)
   = unspotted underside female form *orpheus* Cross 1936 TL Deer Creek Canyon, Jefferson Co., Colorado
d. *rusticus* (W. H. Edwards) 1874 TL Big Trees, Calaveras Co., California (California only, larger in size, underside brownish-gray, hostplant *Rhododendron*)
   Unspotted underside female form *silvius* (W. H. Edwards) 1874 TL Yosemite Valley, Tuolumne Co., California

(The Eurasian relatives are of interest. The male genitalia of European *P. c-album* L. is like that of *P. progne* in all parts, except that the elbow of each gnathos is somewhat enlarged, more bulbous, in *c-album*. The gnathos and tegumen of European *P. egea* Cramer are like those of *P. progne* but the valva is much different. The *P. faunus* genitalia differs from that of *progne* in the gnathos and valva.)

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Reproductive Diapause in *Speyeria* (Lepidoptera: Nymphalidae)[1]

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Abstract. A delay in ovarian development (reproductive diapause) occurs in adult females of *Speyeria coronis* (Behr) and *Speyeria zerene* (Boisduval) from California during the warm-dry weather of the summer flight period. Females copulate soon after emergence; males show little evidence for a delay in spermatogenesis. Termination of the female diapause is hastened by injection of juvenile hormone and by exposure to short-day photoperiods. Diapause delays the onset of oviposition until later summer or early fall and thus decreases the exposure time of overwintering first instar larvae to desiccating conditions.

Introduction

Speyeria Scudder is a North American genus of Nymphalid butterflies characterized by their univoltinism, exclusive use of violets (*Viola* sp.) as host plants, and overwintering as diapausing first instar larvae. There are at least 14 closely related species, 10 of which occur in California (Brittnacher et al., 1978).

Edwards (1874, 1897) found that females of several species from the Eastern US, *S. cybele* (Fabr.), *S. diana* (Cramer), and *S. aphrodite* (Fabr.), mate immediately after emerging from May through July but often do not become reproductively mature and commence oviposition until August or September. These observations strongly suggest a reproductive diapause (Beck, 1980; Masaki, 1980) but no subsequent investigations have been made on the Eastern *Speyeria*. While studying the genetic relationships (Brittnacher et al., 1978) and reproductive biology of Western *Speyeria*, I observed that *S. coronis* (Behr) and *S. zerene* (Boisduval) from California display a similar prereproductive delay. In this paper I document the reproductive diapause of *S. coronis* and *S. zerene* and present results of laboratory studies on the environmental and endocrine bases for diapause termination.

Materials and Methods

Females of *S. zerene* were obtained from the following California localities during the summers of 1973-1975: Boggs Mountain State Forest nr. Cobb, 850 m, Lake

Co. (BM); Mt. Ingalls, 2500 m, Plumas Co. (MI); Fales Hot Springs, 1.5 mi. W
Devils Gate Pass, 2300 m, Mono Co. (FH), and Yuba Pass, 2000 m, Sierra Co.
(YP). *S. coronis* females were collected at (MI) and (YP) during the same
years.

The subspecies collected and locations are as follows: *S. zerene zerene* (Bois-
duval) (BM), *S. zerene conchyliatus* (Comstock) (MI, YP), *S. zerene malcolmi*
(Comstock) (FH), and *S. coronis snyderi* (Skinner) (MI, YP). The peak flight
times, and availability of fresh females, of the high elevation Sierran *S. zerene*
populations occurred approximately one month after the Coast Range (BM) pop-
ulation (July 1 vs. August 1).

A total of 211 butterflies was used in this study. Collections were made using a
standard aerial insect net. Live individuals were placed into glassine envelopes in
the field and returned to the laboratory under refrigeration. Only insects in freshly
emerged condition, based upon wing wear and scale loss, were used in the
experiments. Live weights were determined on a sample of *S. zerene* females
collected in 1975 at the BM locality.

The reproductive status of freshly emerged females of *S. zerene* from BM, FH,
MI, and YP and *S. coronis* from MI was determined by dissecting abdomens in 70%
ETOH. Ovarioles were inspected for oocyte development and mature oocytes
(oocytes with a ridged chorion) were counted and recorded. The condition and
general magnitude of the fat body was observed but not quantified.

To determine the length of the preoviposition period, females of *S. zerene* (BM,
YP) and *S. coronis* (YP) were individually maintained in one-liter cardboard con-
tainers. Leaves of *Viola papilionacea* Pursh served as the oviposition substrate. To
maintain leaf succulence, cut ends of leaf petioles were inserted through a hole in
the bottom of each container into a jar of water. Adults were fed once daily on a 10%
honey-water solution using a holding device described earlier (Sims, 1979), and
maintained under either a LD 15:9 or a LD 12:12 photoperiod cycle at 24 ± 1 C
within Percival environmental chambers. At the 38°N latitude encompassing the
study populations, the chosen photoperiods approximately represent the natural
day length from June 15 - July 15 and from September 15 - October 1.

The time interval between initial exposure to violet leaves and date of first
oviposition was used as a descriptor of reproductive diapause length in *S. coronis*
and *S. zerene*. This seemed reasonable since females of both these and other
Speyeria species that are reproductively mature (i.e. those with mature oocytes)
show no additional behavioral delay of oviposition within the containers used here
(Sims, unpubl. data).

An endocrine basis of reproductive development in *S. zerene* (BM) was studied
using juvenile hormone III (JH III) obtained from Zoecon Corp., Palo Alto, CA. A 5.0
ul capacity microsyringe was used to inject 32 females with 3 ug JH III in 3 ul of pure
olive oil carrier. Olive oil alone was injected into 28 controls from the same popula-
tion. Injection was made along the abdominal pleurite area on the day
following capture.

To examine the effect of day length on reproductive diapause, the experimental
(JH III + olive oil) and control (olive oil) groups were divided with half the females
in each being maintained at LD 15:9 and LD 12:12, 24 ± 1 C. The oviposition re-
sponse of 5 additional non-injected *S. zerene* (BM) females was determined at LD
12:12. Maintenance of females and egg monitoring was performed as pre-
viously described.

Results

The reproductive condition of freshly emerged females from one *S. coronis* and four *S. zerene* populations is shown in Table 1. Only *S. zerene* from the eastern Sierra Nevada (FH) showed signs of reproductive maturity such as mature oocytes and partial depletion of the fat body. All other populations of both species lacked visible oocyte development while fat body completely filled the abdominal cavity. All females had mated at least once as indicated by the presence of a spermatophore in the bursa copulatrix. Three *S. zerene* (2 FH, 1 MI) had mated twice and contained two spermatophores. One of the 3 *S. coronis* and 85/113 (75%) of the *S. zerene* had hardened mating plugs of accessory gland material typically extending to the ostium bursae.

S. coronis (YP) females had a significantly longer preoviposition period at LD 15:9 than either of the two *S. zerene* populations (BM, FH) (Table 2). *S. zerene* females from the eastern Sierra Nevada (FH) had a shorter preoviposition period than the central Coast Range (BM) population. This finding corresponds to the relatively advanced state of reproductive maturity found among young FH *S. zerene* females (Table 1).

The data indicate that relatively short photoperiods decrease the length of the preoviposition period (Table 2). When the statistically homogenous (injected controls and non-injected) values for individuals at LD 15:9 and LD 12:12 respectively are combined and compared between photoperiods, the difference between means (LD 15:9 = 23.00 ± 1.63 days; LD 12:12 = 17.78 ± 1.13) is significant (t = 2.52, 40 df, $p<0.02$).

The mean live weight of *S. zerene* females studied from BM was 0.44 ± 0.10 (1 SD) g (n = 46). The insects were therefore injected with a dosage of JH approximately equal to 7 ug per g of body weight. This dosage is similar to that used to study reproductive diapause in other butterfly species (Pan and Wyatt, 1971; Herman and Dallman, 1981). Injection of

Table 1. Reproductive status of freshly emerged females of *S. coronis* and *S. zerene* from California.

Species	Population	Collection date (1973)	Sample size	Mean number of mature ova in ovarioles ($\pm$1SE)
S. coronis	(MI)	8 July	3	0
S. zerene	(BM)	4 July	31	0
S. zerene	(MI)	8 July	40	0
S. zerene	(YP)	26 July	10	0
S. zerene	(FH)	7 August	32	25.6 ± 5.3

Table 2.   Preoviposition periods of *Speyeria coronis* and *Speyeria zerene*.

Species (population)	Treatment (photoperiod- JH injection	Sample size	Mean number of days to first oviposition $(\pm 1SE)$[b]
S. coronis (YP)	LD 15:9 No injection	9	36.00 ± 3.27 a
S. zerene (BM)	LD 15:9 No injection	13	25.23 ± 2.35 b
S. zerene (BM)	LD 12:12 No injection	5	20.20 ± 2.31 bc
S. zerene (BM)	LD 15:9 - Control[a]	10	20.10 ± 1.91 bc
S. zerene (BM)	LD 12:12 - Control	14	16.92 ± 1.26 c
S. zerene (BM)	LD 12:12 - JH	16	12.37 ± 1.27 d
S. zerene (BM)	LD 15:9 - JH	10	11.20 ± 1.37 d
S. zerene (FH)	LD 15:9 No injection	8	6.25 ± 0.86 e

[a]Controls injected with olive oil carrier alone.
[b]Means followed by the same letter are not significantly different at 0.05 level (Duncan's Multiple Range Test).

juvenile hormone significantly reduced the preoviposition period of *S. zerene* at both LD 15:9 and LD 12:12.

Discussion

Reproductive dormancy of the estival type has been documented in the Lepidoptera groups Satyrinae and Noctuidae (Jacobson, 1960; Scali, 1971; Edwards, 1973; Weissman, 1972) but appears to be unrecorded among the Nymphalinae. Delayed ovarian development with estivation is one method for avoiding hot, dry, and often host plant-deficient summer conditions which could decrease larval survivorship. Small (1-2 mm) first instar diapausing larvae of *S. coronis* and *S. zerene* are particularly susceptible to death from desiccation despite their use of protected overwintering sites in the soil or within plant material and replenishment of lost body fluids by drinking water (Sims, unpubl.). Populations of *S. coronis* and *S. zerene* are characteristically found in xeric habitats of the Sonoran and Transition Plant Life Zones and eggs are laid on or near violets in these areas (Hammond, 1981). Reproductive diapause in *S. coronis, S. zerene* and perhaps other *Speyeria* species may have evolved as a means to reduce the exposure time of first instar larvae to the withering conditions of summer. This contention is supported by evidence for interpopulation variability of adult diapause intensity in *S. zerene*. Diapause

variability appears to correspond to the duration of summer and desiccation stress within the larval habitat as well as the emergence and flight time of adults. The FH population, for example, which flies about one month later, at a higher elevation, and in cooler and moister summer climate than the BM population, shows a weaker diapause response.

The mode of diapause induction is unknown. Initiation of larval development is synchronized with the growth of new violet foliage in early spring and proceeds under fluctuating warm-cool temperatures and increasing day lengths. Adults emerge under long-day warm conditions.

Photoperiod appears to be important in diapause termination and initiation of oogenesis. Short days facilitate diapause cessation and act as a reliable environmental signal for diapause termination. Day length and perhaps other unstudied factors may exert their diapause-terminating effect(s) by reactivating the corpora allata which produce JH. The response to JH found here is similar to that displayed by other Nymphalids with hibernal diapause (Endo, 1970; Benz, 1972; Herman and Bennett, 1975; Herman and Dallmann, 1981). A more detailed comparison of the similarities between the endocrine bases of estival and hibernal diapause in Nymphalids, however, remains to be done.

Males emerge slightly before females at the start of the flight season in each population. An uneven sex ratio is thus established beginning with a preponderance of males and ending with mostly females. Using wing wear as an approximation of insect age, both males and females appear to be sexually receptive soon after emergence. All fresh condition females observed had already mated and three *S. zerene* (BM) males collected in copula were also in fresh condition.

At least a 3 to 5 week long female reproductive dormancy is likely under field conditions during July and August. These are the warmest and driest months in the *Speyeria* habitat of cismontane California (Dale, 1966). The behavior of females during this time is unknown but may differ between the two species. *S. coronis*, for example, is highly vagile and is often seen miles from suitable oviposition sites (Hammond, 1974). Diapause in *S. coronis* may represent an oogenesis-flight syndrome (Johnson, 1969) in which dispersing individuals are reproductively inactive. *S. zerene* generally seems to be less vagile but late season (Sept.-Oct.) captures of females away from breeding sites in California suggest considerable inter-intrapopulation variability in adult movement (Mattoon, pers. comm.). A comparison of reproductive diapause between the Western and Eastern *Speyeria* species would help to clarify the evolutionary basis for this adaptation.

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Stubby-winged Mutants of *Limenitis* (Nymphalidae) — Their Occurrence in Relation to Photoperiod and Population Size

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Abstract. Stubby-winged mutants occurring in *L. archippus* and in two forms of *L. arthemis* are reported and described. The genetic control of this character differs in the two closely related species, involving a single autosomal locus in a Maryland strain of *L. archippus*, and two separate loci in an inbred Vermont strain of *L. arthemis*. Phenotypic expression of this trait may be related to external factors such as larval exposure to long diel photoperiod or to pathogens and local reductions in population size.

Introduction

The occurrence of shortened or "stubby-winged" mutants among Lepidoptera has been reported previously among five economically important moths (Robinson, 1971). These include the pyralids *Anagasta kuehniella* (Zeller) and *Galleria mellonella* (L.), the lasiocampid, *Lasiocampa quercus* L., the selidosemid *Cocallis elinguaria* L., and the bombycid, *Bombyx mori* L. Such mutants possess rounded wings, the base to apex distance being considerably fore-shortened. Often this condition is apparent in the pupal wing-disks prior to adult emergence. In both *Anagasta* and *Bombyx* several genes are involved in the expression of this trait. I know of no similar reports of this condition among butterflies. Totally "wingless" forms, however, have been reported in two pierids: *Pieris napi* L. (Bowden, 1963) and *Tatochila sterodice* Stgr. (Shapiro, 1983).

The purpose of this paper is to report shortened or stubby-winged mutants encountered while collecting, breeding and rearing eastern North American *Limenitis (Basilarchia)* butterflies. I have recently reviewed the evolutionary relationships of the nearctic species of this genus (Platt, 1983). Stubby-winged mutants have been found in the Viceroy, *L. archippus* (Cramer) from Maryland, the banded purple, *L. arthemis arthemis* (Drury) from Vermont, and the red-spotted purple, *L. arthemis astyanax* (Fabricius) from Maryland. The nature of stubby wings in each of these butterflies will be described.

L. ARCHIPPUS (Cramer)

From January through June 1976, I reared a number of broods of *L. archippus* and *L. arthemis-astyanax* at the University of Liverpool in England. These strains were established by rearing third instar (half-grown) diapausing larvae from hibernacula collected along small streams on the U.M.B.C. campus in Catonsville, Baltimore County, Maryland. *Limenitis* larvae enter facultative diapause during the late summer and fall months in response to short daylength and overwinter in hibernacula constructed from silk-covered tubular bases of willow leaves. The numbers and kinds of hibernacula collected, and adults reared from them are given in Table 1. Larvae were induced to emerge from the hibernacula on two separate occasions, and were reared subsequently on fresh leaves of weeping willow (*Salix babylonica* L.) from the nearby Ness Gardens. Detailed methods for overwintering hibernacula, diapause termination and rearing the larvae have been published previously (Clark & Platt, 1969; Kean & Platt, 1973; Frankos & Platt, 1976).

Table 1. Hibernacula collected in Catonsville, Maryland and adults reared from them in Liverpool, England, during April-May 1976.

Larval Group	Date Collected	Foodplant	No. & Percent Hibernacula with Larvae		No., Kinds & Percentages of Adults Reared	
			Live	Dead	*L. archippus*	*L. astyanax*
I. (n=34)	23 XII 75	*Salix fragilis*	25 (74%)	9 (26%)	8 (4mm, 4ff)	2mm (40%)
II. (n=14)	13 I 76	*S. fragilis & S. dispar*	9 (64%)	5 (36%)	7 (4mm, 3ff)	0 (78%)
III. (n=7)	13 I 76	*Prunus serotina*	6 (86%)	1 (14%)	0	2mm (33%)

Note: Larvae were induced to emerge from hibernacula on 18 March (Groups I and III) and on 9 April, 1976 (Group II). all emerging adults possessed perfectly formed normal-sized wings.

The first rearing experiments were begun in late March. Hibernacula were opened, and those containing live larvae were placed in cups containing fresh willow leaves. Unfortunately, these Group I and III larvae were reared under the ambient photoperiod for Liverpool (53° 29' N. latitude). At this time of year the ambient photophase passes through the critical range for Maryland viceroys going from short-day (12 hr daylength) to long-day (14 hr daylength) between 18 March and 16 April

(Duncombe, 1966). Thus, many of the developing larvae died while molt-ing to the 4th and the 5th instars, as well as during the larval-pupal ecdysis, probably as a consequence of this environmental change (see Clark & Platt, 1969, for a discussion of photosensitivity of *Limenitis* lar-vae, and Hong & Platt, 1975, for consideration of the photoperiodic threshold dependence upon latitude among different viceroy strains). Only ten Group I adults (40% of the live larvae) and two Group III adults (33%) were reared successfully.

Earlier studies revealed that developing viceroy larvae often die during molting when the photophase to which they are being exposed is abruptly altered (Platt, unpubl. data). This effect probably results from disruption of the normal neurosecretory rhythms involving the controlling hormones (e.g.: ecdysone and juvenile hormone), the proper diel timing and sec-retory onset of which is important to successful molting in these insects. Beck (1968) believes that photoperiod regulates the temporal organiza-tion of the entire physiological system underlying insect development, rather than having direct effects on insect growth itself (see Ingram, 1976). However, the larvae which died in Liverpool did so while molting, and they showed symptoms and behavior like those of larvae that had experienced abrupt photoperiod alterations.

Later, during April 1976 the second set of rearing experiments was begun, using the Group II hibernacula. These larvae were reared under long-day conditions only, and the rearing was more successful (78% of the larvae survived to eclose as adults). All three of the emerging adult females were hand-paired (modified method of Platt, 1969), two of them being bred to the same male. These pairings are comparable to matings which might have occurred in nature (had the hibernacula not been collected), since all of the larvae began their development in the wild. The matings lasted from 1½ to over 4 hours, which is normal for North American *Limenitis*. After pairing, each female was confined separately and allowed to oviposit on *S. babylonica*. Each female lived for nearly three weeks.

Table 2 presents the rearing results from these broods. Stubby-winged mutants were first noted in Brood 1 as the larvae matured and pupated. The wing disks of these pupae were only about two-thirds as long as those of normal ones (Fig. 1), and a large "naked" area on the ventro-lateral region of each was apparent. This naked area was just anterior to the nor-mal abdominal segments, and was covered only by a thin cuticular mem-brane. Consequently, most of these pupae soon collapsed and dried up. Butterflies developed in several others, but then died before emerging.

Just four mutant butterflies eclosed (Fig. 2). These insects expanded their wings as much as possible. Although unable to fly, these stubby-winged butterflies lived for several days, and were able to feed, hop, and crawl around their cages. Two attempts to hand-pair the mutant males to

Table 2. Numbers in F$_1$ broods of *L. archippus* lab-reared in Liverpool, England during May and June, 1976 on LD photoperiod. Broods 1 and 2 have the same individual male parent.

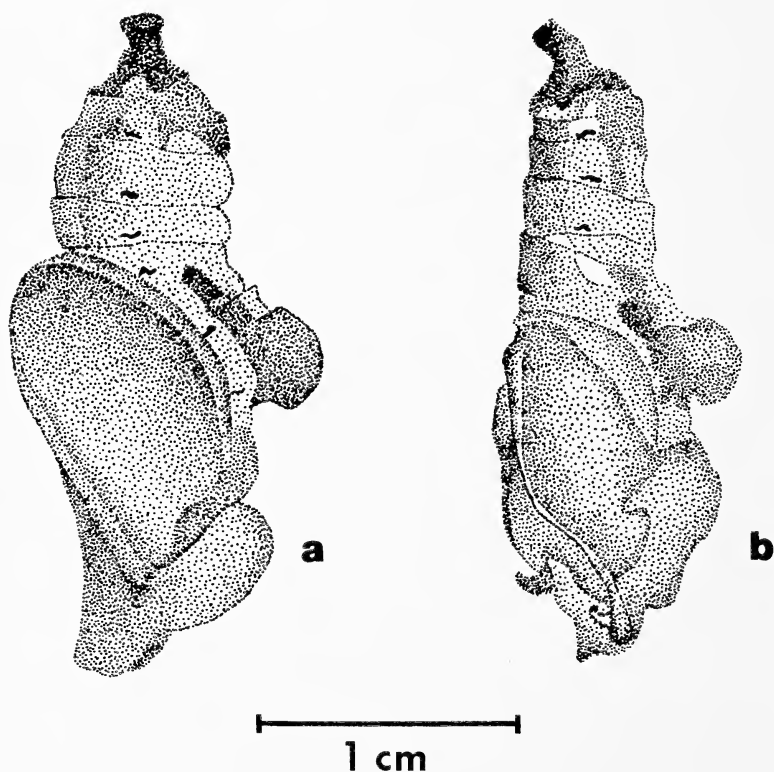| Brood No.	Eggs	Larvae Hatching	Adults (A) & Pupae (P)		Totals
			Normal	Stubby-winged	
1	242	224 (93%)	86 (A)	31 (P) [2mm, 2ff (A)]	117 (A&P)
2	243	231 (95%)	>100 (A)	0	>100 (A)
3	207	184 (89%)	> 90 (A)	0	>90 (A)

1 cm

Fig. 1. a) Normal, and b) mutant stubby-winged pupae of *L. archippus* (Cramer) from Brood 1, U.M.B.C. strain reared in Liverpool, England, in 1976 under LD photophase. Drawings from preserved specimens by Jennifer A. Gurany.

normal female sibs failed. Their siblings with normal wings were easily paired, and ten additional crosses were made. These ten females were released in a roof-top greenhouse, where they proceeded to oviposit on potted willows. The females were observed to fly around the greenhouse at random while ovipositing. Each time one landed on a leaf it "drummed" vigorously with its reduced foretarsi. This behavior was immediately followed by uncoiling the proboscis and "tasting" the abraded leaf surface with the sensory tip of the feeding tongue. Only when the leaf was a willow leaf did oviposition follow (see Platt, 1980 for a more detailed discussion of the oviposition sequence). The viceroy strain maintained itself through August, when it died out. Whether or not other mutant pupae arose from these matings is unknown, since I had by then returned to the U.S.

The observed numbers of normal vs. stubby-winged mutants conform to a 3:1 Mendelian ratio [n (normal) = 86, n (stubby) = 31; EX^2_1= 0.07, p = .78]. Thus, the stubby-winged condition probably results from a single recessive autosomal gene in *L. archippus*. Both the normal winged wild-collected individuals that had been bred to produce Brood 1 are likely to have been heterozygotes, each carrying a single (unexpressed) recessive gene for this trait. The male of Brood 1 also was the P_1 male of Brood 2, in which no mutants appeared. The Brood 2 female was likely homozygous dominant at this locus.

Field observations of ovipositing female *Limenitis* indicate that *L. archippus* females seek out small willow shrubs or poplar saplings, laying from one to several single eggs per plant, before flying on in search of other plants. The wide dispersal of eggs by each female is an important survival strategy for all species within this genus. Each egg is carefully placed by itself on (or near) a leaf tip, usually on the upper surface (Platt, unpubl. obs.).

Therefore, it seems likely that Brood 1 represents the chance hand-pairing of two sibling individuals, for the following reasons. First, my students and I have heavily collected viceroy and red-spotted purple hibernacula from along the streams, marshy spots, and drainage areas on the U.M.B.C. campus each winter since 1970. Thus, we are familiar with nearly all of the areas where the female butterflies oviposit within the campus environs; these consist mainly of woods-open meadow ecotones in the early and middle stages of old-field succession. Often well over 100 hibernacula are collected from the small scattered willows found in this 476 acre area. Removal of most of the available hibernacula from campus each winter means that the local population must be maintaining itself through the migration of bred females onto the campus from surrounding regions. These consist mainly of deciduous woods and suburban neighborhoods. A few stray colonizing females then could introduce most of the eggs into the newly established annual populations each fall, result-
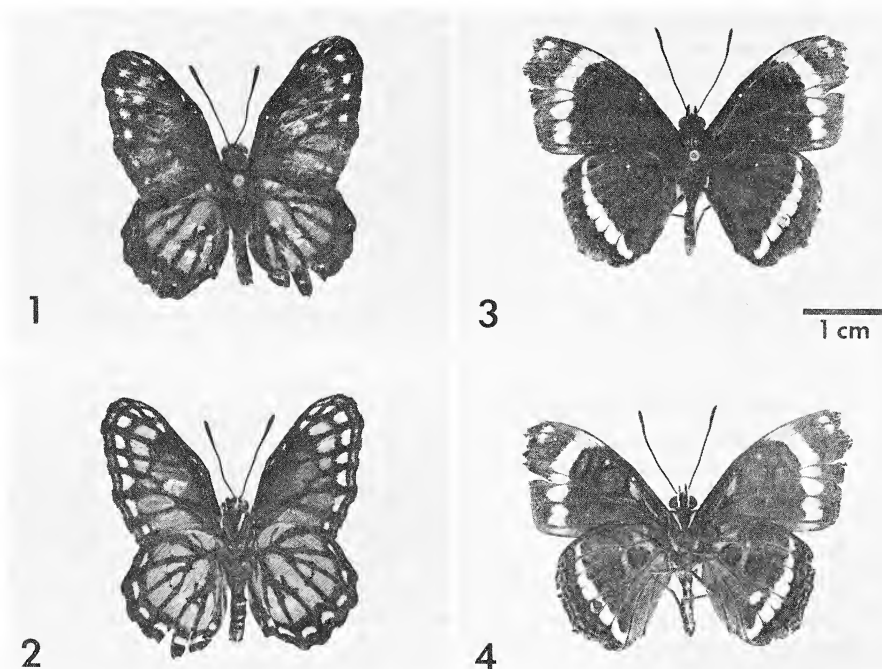
Fig. 2. Stubby-winged mutants of *Limenitis*: 1) and 2) dorsal and ventral aspects of *L. archippus* (Cramer). F$_1$ male from U.M.B.C. campus strain (Brood 1) reared in Liverpool, England, in 1976; 3) and 4) dorsal and ventral aspects of male *L. arthemis* (Drury), inbred Vermont strain reared in 1977.

ing in Founder effects; 3) Third, the two individuals bred to produce Brood 1 were collected in hibernacula obtained on a single day. Only a total of 14 hibernacula were found in the sublocality searched. Thus, it seems that these larvae well could be the progeny of one or two females which had visited this area during the previous autumn. One of these females possessed the mutant allele in a heterozygous condition, either in her own egg cells, or within the sperm cells she obtained from the male with which she had mated. This being the case, we would expect half of her progeny themselves to be heterozygous for this condition.

If these sibs then were to be inbred at random, one would expect one-fourth of the crosses to be between heterozygous sibs, and three-fourths of them to involve either one or two homozygous (dominant) individuals. The results shown in Table 2 are consistent with these ratios: Brood 1 yielded 25% stubby-winged individuals (in the pupal stage), whereas, broods 2 and 3 produced only normal-winged progeny. The above

Table 3   Occurrence of stubby-winged mutants in six broods of an inbred strain of Vermont Limenitis arthemis, 1977 data. Chi square analyses I-IV test for maximum likelihood probabilities (ML) for ratios expected if either a single locus or two loci are involved in the expression of stubby-wings.

Brood	Generation	Wing Phenotypes Normal	Stubby	Totals	Ratios:	Statistical Analyses (Chi Square) I (single gene) 1:1	II (single gene) 3:1	III (two genes) 7:1	IV (two genes) 15:1	Significance
1) 869	G_4 (out-cross)	5 (1mm :4ff)	1m	6	Exp. $\Sigma\chi^2_1$ P=	(3.0:3.0) 2.67 .10	(4.5:1.5) 1.29 .26	(5.25:0.75) 0.67 .43(ML)	(5.62:0.37) 1.11 .31	I-IV,N.S.
2) 874	G_4 (sib-x)	66 (35mm :31ff)	7 (4mm :3ff)	73	Exp. $\Sigma\chi^2_1$ P=	(36.5:36.5) 47.68 < .001	(54.75:18.25) 9.25 <.001	(63.88:9.12) 0.57 .46(ML)	(68.44:4.56) 1.39 .24	I*** II*** III-IV,N.S.
3) 875	G_4 (sib-x)	49 (23mm :26ff)	1m	50	Exp. $\Sigma\chi^2_1$ P=	(25.0:25.0) 46.08 < .001	(37.5:12.5) 14.11 .001	(43.75:6.25) 5.04 .024	(46.88:3.12) 1.54 .22(ML)	I-II*** III* IV,N.S.
4) 877	G_5 (sib-x)	11 (3mm :8ff)	1m	12	Exp. $\Sigma\chi^2_1$ P=	(6.0:6.0) 8.33 < .001	(9.0:3.0) 1.78 .20	(10.5:1.5) 0.19 .69	(11.25:0.75) 0.09 .76(ML)	I*** II-IV,N.S.
5) 883	G_5 (out-cross)	25 (10mm :15ff)	2mm	27	Exp. $\Sigma\chi^2_1$ P=	(13.5:13.5) 19.59 < .001	(20.25:6.75) 4.46 .036	(23.62:3.38) 0.64 .44	(25.31:1.69) 0.062 .78(ML)	I*** II* III-IV,N.S.
6) 918	G_6 (out-cross)	20 (12mm :8ff)	2mm	22	Exp. $\Sigma\chi^2_1$ P=	(11.0:11.0) 14.73 < .001	(16.5:5.5) 2.97 .08	(19.25:2.75) 0.50 .48	(20.62:1.38) 0.30 .61(ML)	I*** II-IV,N.S.
All Broods		176 (84mm :92ff)	14 (11mm :3ff)	190	Exp. $\Sigma\chi^2_1$ P=	(95.0:95.0) 138.13 .000	(142.5:47.5) 31.50 .000	(166.25:23.75) 4.57 .034	(178.12:11.88) 0.41 .53(ML)	I-II*** III* IV,N.S.

explanation offers the only logical reasons for why I might have crossed two wild-collected individuals, each bearing the same recessive mutation in a heterozygous state.

LIMENITIS ARTHEMIS ARTHEMIS (Drury)

Other stubby-winged mutants arose in a strain of *L. arthemis* descended from four wild-caught females collected at Starksboro, Addison Co., Vermont, in June and July 1976 (Fig. 2). Eggs were obtained from these females, and their progeny were reared in the laboratory at U.M.B.C. The strain was maintained by inbreeding (sib-pairings) and by out-crossing non-sibs. Six 4th through 6th generation broods yielded a total of 14 stubby-winged individuals (Table 3). These broods were lab-reared on *Salix babylonica* between January and May 1977, at room temperature on a 18L:6D photoperiod. A total of 884 *arthemis* were reared during these experiments which included 31 separate broods. The number (x ± s.e.) of progeny in these broods was 28.5 ± 4.7 individuals, with the corresponding values for each sex being males = 14.9 ± 2.5, and females = 13.6 ± 2.3. The sex ratios approach 1:1 in all generations, with most having a slight (non-significant) excess of males. No excessive pupal mortality of the kind encountered in the *L. archippus* strain from Maryland was observed.

The data from each of the six broods as well as the overall totals give maximum likelihood fits to either 7:1 or 15:1 ratios of normal-winged:stubby-winged specimens, respectively, suggesting that these inbred *arthemis* mutants result from two unlinked recessive autosomal loci. The six broods yielding stubby-winged individuals all can be traced back to a single third generation brood which yielded all normal-winged individuals. These normal-winged butterflies presumably included a high proportion of double heterozygotes resulting from prior inbreeding. Once these double heterozygotes are cross-bred the double recessive homozygotes with stubby-wings will appear in subsequent broods. Those individuals having either one or two wild-type alleles at each of the two loci will be of normal wing phenotype, whereas the double recessive homozygotes will be stubby-winged. There is no evidence for sex ratio disturbance among these broods, so that differential lethality does not appear to influence these results. Among these *arthemis* broods the pupal wing pads are fore-shortened, similar to the way they were among the *archippus* mutants described above. These stubby-winged *arthemis*, unlike their *archippus* counterparts, however, were perfectly capable of flying about our lab cages, despite their reduced wing size. Wing reduction in these *arthemis* appears to affect mainly the outer one third of their wings, rather than the entire wings, as in *archippus*.

Assuming random selection of the various parental genotypes during further inbreeding, one would expect to obtain only normal-winged

individuals from 66% of the crosses. Another 25% of the crosses (those involving two double heterozyous parents) would be expected to yield both normal and stubby-winged individuals in 15:1 ratios. Finally, 9% of the crosses (those involving individuals homozygous recessive at one locus, but heterozygous at the other), should throw either 7 normal : 1 stubby, or 3 normal : 1 stubby, depending on how the respective alleles are distributed in the two parents (Table 4).

Maximum likelihood probabilities for the six broods throwing stubby-winged individuals shows that two conform most closely to the 7:1 ratio, whereas, the remaining four fit the 15:1 ratio most closely (Table 3). Close fits to the 3:1 ratio, which result from one of the two loci becoming homozygous recessive in both parents were not observed. The data presented in Table 3 rule out the possibility that a single autosomal locus controls stubby-wings in this *arthemis* strain. Rather, this trait appears to be under the control of two separate autosomal loci. The sex ratios among the six broods yielding stubby-winged individuals all approach 1:1 with the overall sex ratio being 95 males:95 females. However, the sex ratio among the stubby-winged individuals themselves is biased in favor of males (11 males:3 females, $EX^2_1 = 4.57$, P = .034). Possibly the phenotypic expression of this trait differs between the two sexes, since the overall sex ratio is undisturbed.

LIMENTIS ARTHEMIS ASTYANAX (Fabricius)

A single male specimen of *astyanax* having matched stubby forewings and normal sized hindwings was hand-netted by P. J. Kean on 27 July 1977 in Anne Arundel Co., Maryland, along Patuxent River Road in Harwood (Fig. 3). Despite its reduced forewings, this specimen was quite capable of flying, and was resting on a tree trunk when it was collected. The forewings of this butterfly are only about one-half the normal length, and their outer margins have a crimped appearance. The symmetry of these fore-shortened wings suggests that their basis is genetic, rather than developmental. Unsuccesful attempts were made to breed this mutant specimen to normal females from our laboratory strains.

DISCUSSION AND CONCLUSIONS

This paper contains the first report of stubby-winged mutants occurring among nymphalid butterflies. A. M. Shapiro (pers. comm.) has had more than one "stubby-winged" gene appear in his colonies of Andean *Tatochila* (Pieridae) which have been maintained at U.C. Davis for the past five years. Earlier he found such mutants in *Colias eurytheme*, and he notes having collected a "semi-stubby" specimen of *L. arthemis* in upper New York State, as well.

It is possible that reduced wing size of this sort may represent a syndrome resulting from pathologic bacterial or viral infections affecting the

Table 4. Frequencies of the various genotypes of normal-winged individuals resulting from crosses involving double heterozygotes, and the probabilities of these genotypes being used in further matings (assuming random selection of the parental genotypes).

Genotypes among Normal-winged Progeny of two Double Heterozygotes	Frequency of Genotypes (among the Normal-Winged Progeny)[1]	Probabilities of the Genotypes being used in Matings between Normal-winged Individuals resulting from A Double Heterozygous Cross[2]
1) 1AABB	0.067	0.13
2) 2AaBB	0.133	0.23
3) 1aaBB	0.067	0.10
4) 2AABb	0.133	0.18
5) 1AAbb	0.067	0.02
Subtotals (1-5)	0.467	0.66 (all normal-winged)
6) 4AaBb	0.267	0.25 (15 normal:1 stubby)
7) 2aaBb	0.133	0.07
8) 2Aabb	0.133	0.02
Subtotals (7 & 8)	0.266	0.09 (7 normal:1 stubby or 3 normal:1 stubby)
Grandtotals (Subtotals, plus 6)	1.00	1.00

[1]The frequencies among normal-winged individuals are based on proportions of 15 rather than 16 since the stubby-winged individuals (genotypes 1aabb) are phenotypically distinct. All other genotypes are normal-winged, and cannot be told apart.

[2]These probabilities are the additive totals of crossing each genotype by itself, and by all others. When two separate genotypes are involved the two frequencies are further multiplied by two, since either sex can be represented by each of the two genotypes involved. As one progresses from genotype one through genotype eight only those specific crosses not previously accounted for are included in the row totals.

insect cultures (Shapiro, pers. comm.). This is most likely to occur when high rates of larval mortality are encountered. In the absence of difinitive genetic data (e.g., breeding from the "stubby-winged" individuals themselves), this possibility cannot be entirely ruled out. However I consider this possibility an unlikely explanation for the occurrences of stubbywinged *Limenitis*, since no such viral afflictions were noted in my cultures.

A second possibility is that the expression of some or all of these mutants is related to rearing larvae under unusually long photoperiod regimes. Insects in general, and Lepidoptera in particular, are very sensitive to photoperiod, and rely upon this environmental cue to regulate their temporal growth processes in seasonally unstable temperate environments (Pease, 1962; Danielevskii, 1965; Beck, 1968). In odonatan (damselflies and dragonflies) nymphs, both photoperiod and temperature have been shown to influence abnormal wing-pad development (Lutz, 1968, 1974; Ingram, 1976). Thus, the expression of the lab-bred stubby-winged mutants in *L. archippus* and *L. arthemis* may be dependent upon the unusually long photphase to which the developing larvae were exposed. Of course, the proper control experiments have not been done to test this hypothesis.

Nevertheless, it is conceivable that the stubby-winged condition might not have been expressed if these insects had been reared under conditions of ambient photophase for the respective latitudes from which the strains originated. If this were true, then the mutant individuals perhaps represent those which have the greatest photoperiod sensitivity among their strains and broods. I note this possibility because it seems likely that the

Fig. 3. Wild-caught Maryland male specimen of *L. arthemis astyanax* (Fabricius) showing stubby forewings.

butterfly genome is strongly canalized against the expression of such mutants when the insects are grown under ambient environmental conditions (Shapiro, 1981). This is not meant to suggest that these stubby-winged butterflies are merely phenocopies. Normal winged adults were always produced along with them in appropriate genetic ratios.

The three closely related admiral butterflies exhibit similar stubby-winged mutant phenotypes, but the genetic control of this trait appears to differ in *L. archippus* and *L. arthemis*. In the former, stubby wings is controlled by a single recessive gene, whereas, in the latter a pair of loci are involved, with the double recessives only expressing this trait. The control of stubby forewings only in Maryland *astyanax* remains unknown, but probably also has a genetic basis. In *Limenitis*, a number of multifactorial loci affecting wing coloration are known to influence either the forewings or the hindwings (Remington, 1958; Platt & Brower, 1968; Platt, 1975, 1983), and it is likely that a similar mechanism is controlling stubby forewings in *astyanax*.

It is equally possible that the two autosomal loci controlling stubby-wings in *L. arthemis* are acting along the same (or related) developmental pathways as is the *L. archippus* locus. For example, stubby wings in *L. archippus* could be represented by locus *A*, with a/a individuals representing the homozygous recessive phenotype. In *L. arthemis* a second locus, *B* could likewise be affecting the stubby-winged phenotype, with doubly homozygous recessive individuals (a/a, b/b) only expressing the mutant phenotype. If so, then this second locus might have become fixed in the Maryland strain of *L. archippus* studied in Liverpool, and the *A* locus alone produces the effect. Such a theory requires either: 1) that the *B* locus has become fixed for the recessive allele in the Maryland *archippus* strain, or 2) if the dominant B allele has become fixed in Maryland *archippus*, then the *a* allele has to have developed differential penetrance in the *archippus* genome, such that it alone (when homozygous) can produce the mutant phenotype.

Finally, it is interesting to note that a few other species of *Limenitis*, as well as a number in the related genera *Ladoga, Neptis, Pantoporia*, and even a few species of *Adelpha* possess wing size which is only about two-thirds that of *L. populi* and the nearctic *Limentis*. The stubby-winged mutant genes, thus, may represent an evolutionary reversion toward a smaller ancestral phenotype still present in these other (more primitive) genera.

These results provide evidence that potentially lethal recessive mutant genes are carried in natural Lepidopteran populations, and that such mutations can be expressed among some individuals, especially when founder effects and inbreeding are involved. Such conditions could arise locally when adult populations are small, following physical environmental stresses, habitat destruction, decimation by disease, heavy predation,

parasitism, and/or collecting pressures, any or all of which may contribute to a population bottleneck.

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The Immature Stages of *Catocala erichi* Brower (Lepidoptera: Noctuidae)

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Abstract. The eggs and larvae of *Catocala erichi* Brower are described, and some notes presented on the larval feeding and resting behavior in the laboratory.

Catocala erichi Brower (1976) was named from specimens collected in the San Bernardino Mountains, California. Walter and Johnson have reared broods from ova of three females collected in the type locality. Descriptions of the immature staes were prepared from the most recent rearing in 1978. In the descriptions of the larvae, the chaetotaxy of Hinton (194) and of Hasenfuss (1963) will be followed (Fig. 4).

Egg. Shape hemispheroidal, somewhat flattened at the microscopically reticulate, polar, micropylar area, the egg base broad, flat. Micropylar area enclosed by a sharp-edged, polygonal ridge, from which sharp-edged ribs radiate down the sides, some ribs forking just below their origin (Fig. 1). Troughs between the ribs crossed by regularly spaced, delicate septa, these continuous around the egg, forming a reticulate sculpturing of the chorion. Egg brown at oviposition, the fertile eggs developing a pattern within the first days; the micropylar area and adjacent surface, light gray, the gray encircled by an interrupted, dark brown band. Basad, half-way down the sides, a light gray, interrupted ring, edged below by another broad, dark brown band. The base, pale brown. Egg diameter, 1 mm.

First Instar Larva. Head dark brown, lighter about the mouth and frontal suture. Setae black, inconspicuous; sutures inconspicuous.

Body dark gray-brown; cervical sclerites dark brown. A wide, longitudinal stripe of lighter color on the dorsum from TII to A10. At its edges, through the D2 setae of TII and TIII and the D1 and D2 setae of A1 to A10, a longitudinal, narrow, dark brown line. Next ventrad a second, wider, heavier, dark brown line through the SD2 setae of TII and TIII and dorsad of the SDI abdominal setae, to A10; light brown between the lines and on the lower border of line 2. The middle and lower sides dark brown, interrupted by light areas. Body setae small, black, from black bases. Thoracic legs dark brown. Prolegs of A5 and A6 with broad, lateral, dark brown stripes.

Second Instar Larva. Head light brown, reticulate with fine, dark brown lines. The front rimmed at each side, anterior to the ocelli, by an interrupted, heavy, black line curving from the vertex ventrad to the antennal base. Setae black, small; sutures inconspicuous.

Body brown. From TI to the anal valve, a wide, light-gray, middorsal line forming whitish spots at the caudal edges of the segments. Setae black, inconspicuous, bases brown. On the sides, four longitudinal, dark brown stripes from TI to A10; upper two stripes narrow, separated by lighter brown; lower two stripes wide, covering the sides to the venter, separated by a narrow, discontinuous line of lighter brown. Laterally, between A5 and A6, an oblique, dark, chocolate brown patch frm the edge of the dorsal midline to the prolegs. Between A6 and A7, a smaller, lateral, dark brown patch, the color continuing on the lower sides of A8 and A9. Thoracic legs banded in light and dark brown; prolegs light gray-brown. Venter pale brown; median spots dark brown, largest on A1 to A4, to TI and A9.

Third Instar Larva. Head as in the scond instar, with these changes: orange protuberances dorsad of the P1 setae; orange lines descending the front from the protuberances to the black A1 setae. Other lower setae white; more dorsal setae black, their bases brown.

Body a rich medium brown. Dorsum almost white, middorsal line narrow, brown, interrupted. Through the dorsal setae, and laterad and ventrad, parallel, longitudinal lines and stripes of light and dark brown, alternating, to the ventral filaments. Ventral filaments light brown. On A5, a dark brown, middorsal tubercle, center light brown. On the sides of A5 and A6, an oblique, chocolate brown patch from the A5 tubercle to the prolegs. On the lower sides of A7 and A8, a dark brown shading. On A8, a transverse dorsal ridge bearing the large D2 setal bases, the ridge edge dark brown, the brown continuing forward briefly on the sides. On A9, a lesser ridge and setae.

Fourth Instar Larva. Largely as in the third instar. The oblique patch on the sides of A5 and A6, rich orange-brown.

Fifth Instar Larva. (Fig. 2). **Head** light brown, reticulate with dark brown lines. Upper setae pale brown; lower setae nearly white. Head bilobed; prominent, orange protuberances at the apices of the vertex lobes dorsad of setae P1. Coronal and frontal sutures paralleled by brown lines. The front rimmed dorsally and laterally by a broad, netted, dark brown line, lighter dorsad, becoming nearly black laterad to the antennal bases. Ocelli I to IV black, V and VI clear. Antennae, mandibles, labrum, lower clypeus, light brown, the mandibles black-edged. Frons-clypeus dorsad, darker brown. Genae light brown.

Body color varying from pale gray-brown, to orange-brown, to dark gray-brown, stippled generally in dark gray and black; pattern lines of variable intensity. Bases of the D2 setae, large, raised, orange; other setal bases raised, brown. Dorsum light brown, middorsal line dark gray, interrupted. Through the dorsal setae, a wide, longitudinal, dark brown stripe from TI to A10, bordered below by a wide, light brown stripe. More ventrad, a third stripe, dark brown, through the SD1 setae, spiracles, and L1 setae. Lower sides paler. On A5, a transverse, dorsal ridge between the D2 setae, bearing the flattened, middorsal tubercle, the ridge and the tubercle orange and brown; D2 setal bases of A5 large, orange. On A8, a transverse, dorsal ridge, bearing large, orange D2 setal bases, the ridge caudal edge dark brown, the brown continuing ventrad and forward beyond spiracle A8. A9, with lesser ridge
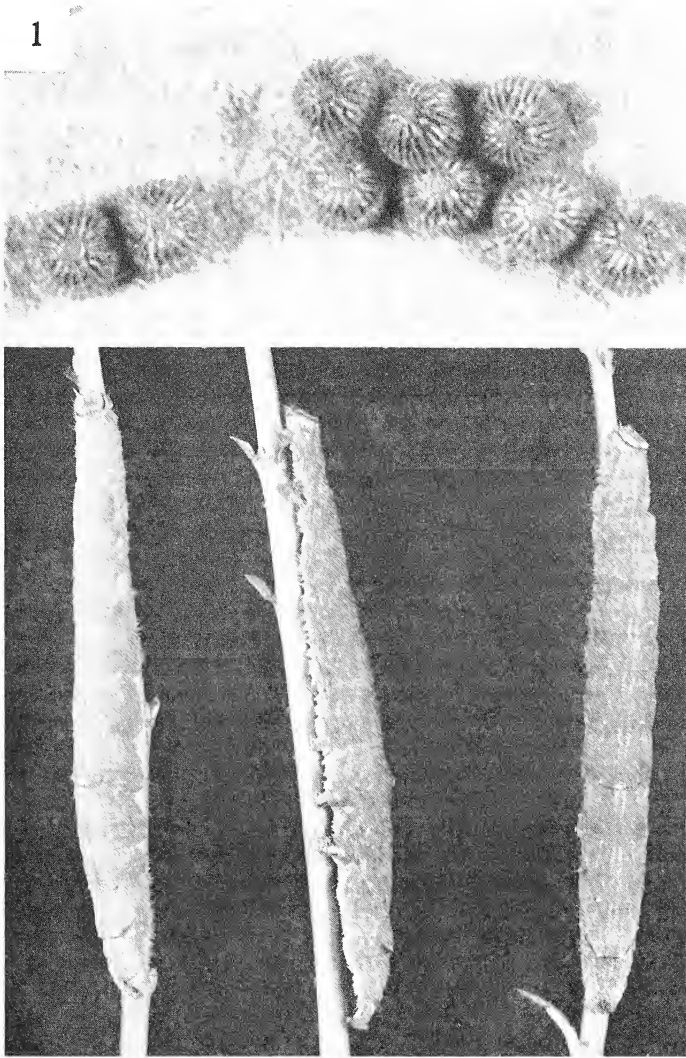
Fig. 1. *Catocala erichi* fertile ova. Diameter 1 mm.

Fig. 2. *Catocala erichi* fifth instar larvae, showing color variations. Length 68 mm when photographed.

and setae. Anal valve orange-brown. Thoracic legs light brown, tibiae black-edged, tarsi dark, accented by light brown. Prolegs pale, yellow brown, a dark spot near bases, vertical dark lines distally. Spiracles pale brown, black-rimmed. Intersegmental folds of A1 to A5, orange-brown. The oblique, lateral patch on A5 and A6 inconspicuous (see Brower, 1976, p. 37). Ventral filaments nearly white. Venter pale yellow-brown; median spots on TI to A9 purplish-black.

Fig. 3. *Catocala erichi* adults. Above: male, 67 mm span. Below: female, 65 mm span. Both adults from the larval brood of Fig. 2.

Rearing Notes. The ova were held overwinter outside under shelter on a north wall, except for a period in refrigeration at about 5°C during January. Hatching was staggered from March 22, 1978, to April 13. Hatching may be expected six weeks later in the mountain habitat. The larvae were reared on *Salix lasiolepis* Benth. (Munz, 1974). For the first larva: eclosion March 22; moults, March 27, April 2, April 8, April 14; spinning, April 25; emergence of an adult male, May 30 (Fig. 3). Larval and pupal periods each 35 days. In nature, no adults have been taken before August 1.

First instar larvae rested closely applied to leaf edges and veins beneath leaves. They fed at all hours. Second instar larvae rested on veins beneath leaves, on rearing box walls, and on cloth-covered openings, the head closely ppressed to surfaces. Feeding, chiefly at night. Third instar larvae rested on foliage, stems, and box walls. Of 31, 11 rested head up, 15 head down, 5 horizontally. Feeding, at night only. Fifth instar larvae were transferred to potted, rooted willow cuttings in net sleeves, outside in full sun. Larvae rested chiefly on large willow stems. On April 13, on willow stems, 18 were head up, 19 head down, on sleeve netting, 4 horizontal. In nature the food plants surely are willow species of the high mountains.
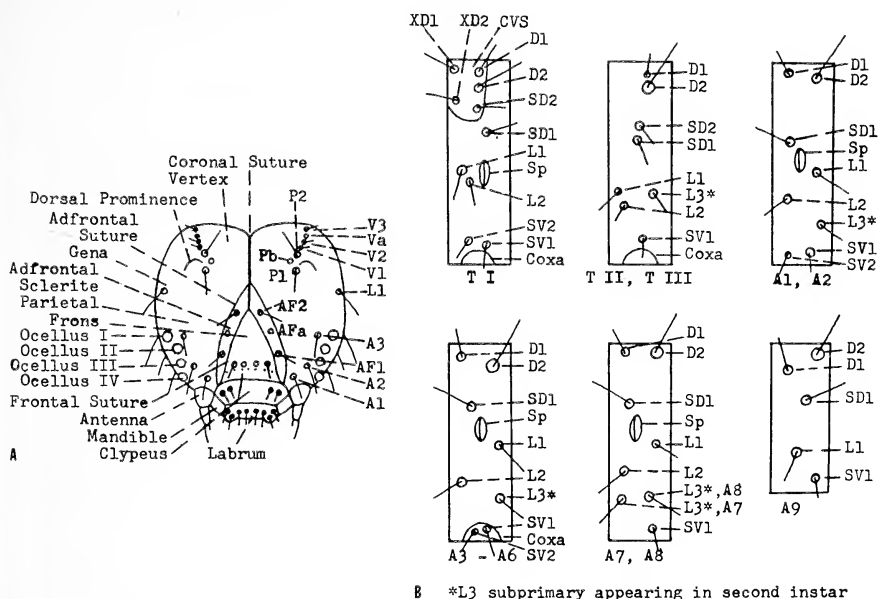
Fig. 4. Chaetotaxy of head and body in *Catocala*, adapted from Hinton and Hasenfuss.

A. Head regions, sutures, setae, and sensoria; setae with capital letter and numeral; sensoria with capital letter and small letter. A, anterodorsal; AF, adfrontal; L, lateral; P, posterodorsal; V, vertex.

B. Setae of thorax and abdomen, segment 10 omitted. CVs, cervical slerites; XD, anterior dorsal tactile setae of TI; D, dorsal; SD, subdorsal; L, lateral; SV, subventral; Sp, spiracle; TI, TII, TIII, thorax; A1 to A9, abdomen.

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Notes

Culture Maintenance of *Vanessa atalanta rubria* (Nymphalidae)

Many lepidopterists do not have access to the laboratory facilities frequently referred to in publications dealing with butterfly culture. While sterile, controlled laboratory conditions may certainly be preferred for long-term maintenance of healthy cultures, they are not a necessity for all species. There is a great deal of work which can be achieved by those with only residential, indoor facilities as places of work.

The project reported in this article was performed in a one-bedroom upstairs apartment which received only 90 to 120 minutes of afternoon sunlight each day. I wished to determine the conditions necessary to establish and maintain a culture of *Vanessa atalanta rubria* (Fruhstorfer) indoors. Because of airborne particles from cooking, cleaning, and other domestic activities, plus fluctuations of temperature, light, and humidity, this environment was neither sterile nor controlled. However, from February to July 1982 I was able to raise four continuous generations of butterflies. The following procedures I hope will motivate and assist others to experiment with the same or other species.

If rearing is to be done in the same room a collection is kept, it is essential that all Vapona™ pest strips, if they are being used, be removed from the residence. This insecticide is very effective even when used in "airtight" cabinets: the vapor escapes when these are opened. In the genus *Vanessa* when early stages are exposed, ova do not hatch and larvae gradually lose the ability to hold onto their foodplants and react by "spinning webs in the air" before dying. The residence must be aired well before livestock is brought inside. I have used paradichloroben-zene (PDB) in small quantities in airtight cabinets to protect my collection without harm to the cultures in the same room. If PDB odor was present after opening the cabinets, the room was quickly aired.

In nature, *Vanessa* butterflies hilltop and sun themselves in the afternoon for territorial reasons noted by Bitzer and Shaw (1979(80), Territorial Behavior of the Red Admiral, *Vanessa atalanta* (L.) (Lepidoptera: Nymphalidae). J. Res. Lepid. 18:36-49) and in preparation for courtship and mating according to Shields (1967, Hilltopping. J. Res. Lepid. 6:69-178). Therefore, a flight cage should be placed in a window with afternoon sunshine. The flight cage used was modified from that used by White (1981, pers. comm.) and measures 51 X 51 X 122 cm (20 X 20 X 48 inches), constructed of one-inch wood frames and nylon netting on all sides except the bottom which is hardboard. An inexpensive cage can be made from a large cardboard box by cutting out the side and top panels, leaving a one to two-inch margin for strength on each edge to which the netting is glued.

Captive *Vanessa atalanta* feed throughout the day. A honey-water mixture was provided in the proportion of 6 to 9 ml of honey to 190 ml of water (1 to 1½ teas-poons honey in 1 cup of water) and was made daily. The mixture was poured into a petri dish and white, unscented tissue paper was added until most of the liquid was absorbed and the tissue remained saturated.

Freshly cut (with a sharp razor blade) stalks of the foodplant *Urtica holosericea* Nuttall (Stinging Nettle) were placed in small jars of water and placed into the cage every one to three days.

On 19 February 1982 ca. 20 larvae of *V. atalanta rubria* were collected on *U. holosericea* growing along a seasonal foothill creek in Barlow Canyon, Ventura Co., California. These were reared to adults which were then placed into the flight cage with fresh nettles and honey-water. The first matings occurred four days after emergence and took place at or soon after sunset. "Sunset" in the room was 90 to 120 minutes before the actual sunset because the neighboring building blocked out the late afternoon sun. The male butterfly located a female, approached her along one side, and vibrated his wings in a nearly closed position. He held one of his antennae forward with those of the female and the other directed posteriorly to her abdomen. He then curled his abdomen so that the posterior tip was directed forward with the genitalia flared. He then attempted copulation. Even if the female walked away from the male, he would run after her in this position. If copulation was successful, the pair became quiescent for the duration of the mating process. Most often this lasted 90 minutes, but occasionally longer, even overnight matings occurred.

V. a. rubria prefers mating at or after sunset, and this twilight effect can be lengthened in duration by using a floodlight above the cage. Both GE 75-watt Reflector Spot and GE Plant Gro and Sho 75-watt Spot lights were used successfully, one at a time. The light was mounted 15 cm above one side of the cage and directed slightly downward across the top netting to the opposite corner. This gave the butterflies a longer period each day to court and mate.

Even within the confines of the flight cage, the males displayed territorial chase behavior, although the flights were limited in area. Very often the males would run after each other instead of fly, and this behavior was quite amusing to observe because it was so unexpected. The first male sat head down, wings closed, on the sunlit side of the cage, and would "watch" another male flying around the cage interior. I use the term "watch" because this male would follow the flight of the other either by short, lateral head movements or by turning his body to direct his eyes forward. If the second male landed nearby (within ca. 30 cm), the first male would run over to him and tap his mesothoracic legs upon the thorax or wing bases of the second male until the second male either ran or gave chase. During times when no males were flying in the cage, a "restless" male seeking a chase would run to another and initiate a chase in the same manner. Less often, three or four individuals would be involved in the same chase. When behaviors such as these are observed in a cage, it is an indication that the butterflies are quite content and courting and mating will most likely take place.

The netting on the side of the cage facing the window was the primary locality for the courting and mating activities, so the foodplants were set back to the middle of the cage. The honey-water dish was placed on the cage floor. Elevated perching sites such as tall, narrow boxes wrapped in paper towels were readily used by sunning individuals, and when honey-water was sprinkled on these the butterflies fed eagerly.

The minimum number of adults in a cage where mating took place was one male and two females. The maximum number was not determined, but cages with 15 to 20 butterflies produced good results. With the use of a floodlight, a total of 8 successful matings occurred among a total of 16 individuals, with some males mating twice. Indoor temperatures during courtships and matings varied from 24° to 27°C. Hand pairing was not attempted.
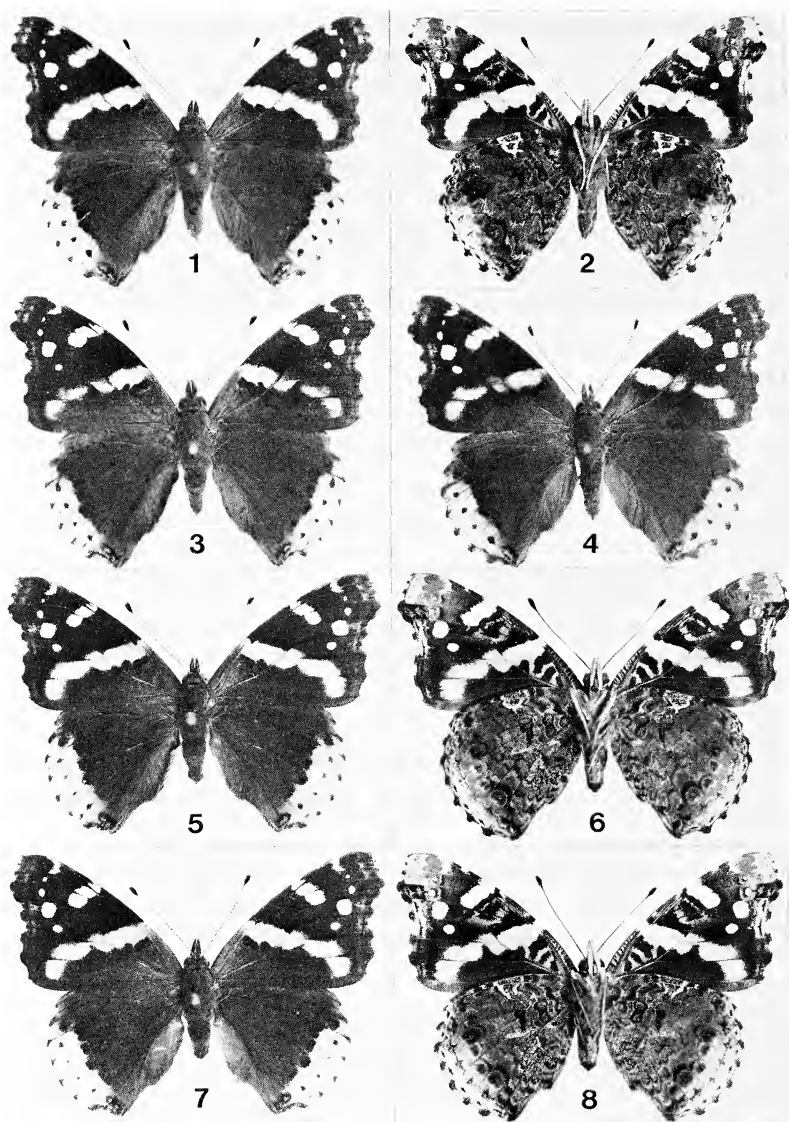
Figs. 1-8. *Vanessa atalanta rubria*, all reared. **Figs. 1 & 2:** typical, normal male from Calif.: Ventura Co.: Barlow Cyn. Elev. 500 ft., 17 December 1978. **Figs. 3-8:** variant phenotypes from culture. Filial generation, sex, dates of emergence (all 1982), and brood labels: **Fig. 3,** F_3 male, 9 July, 3B; **Fig. 4,** F_3 female, 2 July, 3BDF; **Fig. 5,** F_2 female, 28 May, 2DC2; **Fig. 6,** F_2 female, 28 May, 2DC2 (different specimen than Fig. 5); **Figs. 7 & 8,** F_3 female, 5 July, 3B.

Wild collected males of both *V. a. rubria* and *V. annabella* (Field) did not adjust to the confinement of the cage. They showed no interest in the unmated females and quickly destroyed their wings flying against the netting. Among the reared butterflies, mating began one day after emergence, but could take place for the first time a week after emergence.

Females began to lay eggs one day after mating. This species is very prolific and can lay over 300 eggs. The duration of the egg stage is four days at indoor temperatures of 24° to 27°C, so on the third day leaves with ova were placed into rearing containers. The foodplant leaves can be cut up when specific numbers of ova are desired in each container. As some of the females aged and became familiar with the cage interior, they gave up any finesse they had with the oviposition process and simply fluttered to the general vicinity of the foodplants, dropped into them, and began laying eggs wherever the abdomen contacted a plant surface. Many laid eggs on the netting, and the resulting larvae were transferred to containers with the use of a fine brush.

Larvae were reared in plastic boxes measuring 111 X 111 X 39 mm (BioQuip Cat. No. 1182A). Six to eight sheets of white, unscented bathroom tissue were placed in the bottom and slightly dampened, and fresh foodplant leaves were placed inside. Setting one flat leaf on top of another provides an easy situation for nest construction by hatching larvae. The tissue was changed and the old foodplant replaced with new as often as needed. The higher humidity inside these boxes keep the foodplants fresh for several days, and larvae mature quickly. Unfortunately these same conditions promoted the development and spread of disease, and great care was taken to remove dead or dying larvae. What was believed to be a polyhedral virus (White, 1981, and Taylor, 1982, pers. comms.) caused heavy mortality in the last instars and pupae in all the generations reared in this project. Had sterilization techniques been used on the ova and foodplants, it is possible the disease could have been stopped. Sterilization procedures currently in use for *Vanessa cardui* (Linnaeus) cultures by White (1981, pers. comm.) require washing the ova in a 5-10% Chlorox solution with 2 drops of jet Dry detergent per 16 oz. of Chlorox solution for 10 minutes, draining, and washing in water for 10 minutes. This procedure also removes the ova from the leaf surfaces, so the ova must be collected with filters. Foodplants must similarly be surface decontaminated.

If sterilization methods are not used, the disease can be largely avoided by transferring the fourth instar larvae from the rearing boxes to cut stalks of foodplants in water in large, airy rearing cages. Contrary to Stone and Midwinter (1975, Butterfly Culture. p. 27, Blanford Press, Dorset, Great Britain, culture instructions for *Aglais urticae* (L.) referred to from *V. atalanta*, p. 31), larvae did not die when reared on cut nettles placed in water. Younger larvae can be transferred if the disease should begin to appear earlier. Rearing cages are preferred if large numbers of larvae are to be reared simply because they are easier to clean than the great number of plastic containers needed to house an equal number of larvae.

The plastic rearing boxes are deep enough to allow the mature larvae to hang freely for pupation from the lid. The larvae usually secure all nearby surfaces with silk webbing before hanging, and this can be carefully cut permitting removal of the lid. Following hardening of the pupa (one day), an area surrounding the cremaster and its silk foundation is scored with a sharp object. The resulting 1-2 cm circle of silk with the attached pupa is removed by pressing adhesive tape onto

the silk foundation alongside the cremaster and pulling the tape off again. The entire foundation usually sticks to the tape which is then reapplied onto the lower surface of a larger cardboard platform which in turn is placed into an emergence cage. Eclosing adults are then examined on a daily basis and those with characteristics desired for breeding are selected. Fresh adults are easily examined when a pencil or probe wrapped in a paper towel dipped in honey-water is placed at the front of the butterfly's mesothoracic legs. It begins feeding and displaying its wings after its feet touch the food.

This culture was terminated in the third week of July 1982 at the end of the third generation as the foodplant resources were in seasonal decline. Balcom Canyon, near Santa Paula, Ventura Co., California, is the site of very large colonies of *Urtica holosericea* and was the source of all foodplants used in this project.

While the main purpose of this work was to establish conditions necessary for maintaining a culture of *V. a. rubria*, some mass selection was accomplished. In one culture, adults with the most constricted red band on the forewing were selected for mating, and four separate lines were maintained. The most extreme results are shown in Figs. 3 and 4. In a second line of breeding, two pairs of F_2 adults with a scale deficiency were bred together, but all the ova failed to hatch. In a third line, an interesting variation occurred in the second generation which differed from typical *V. a. rubria* in the following ways (Figs. 5 and 6): a slightly modified wing shape; on the upperside, a wider marginal red band on the hindwing with protruding ocelli; and on the underside, increased brown coloration of most of the mottling pattern elements and reduced size of the ocelli. This variant was informally referred to as "brunnea" in the culture. Two pairs of adults of this variation were bred together and from the two females over 800 ova were obtained in two weeks. Unfortunately, exact numbers of the resulting phenotypes were not recorded as the entire project had reached such overwhelming numbers by this time that except for simple cage maintenance, all other activities were severely limited. General observations of the F_3 showed the majority to be phenotypically like the F_2 parents, but many had greater purplish-blue development in place of the brown, and others had the hindwing upperside band yellowish instead of red (Figs. 7 and 8). Another variant unlike the parents occurred in about one-fourth of the F_3: it had a bright pinkish-orange cast to the upperside bands, a nearly normal underside, and normally-shaped wings.

The few examples above only hint at the multitude of possibilities for genetic research, in addition to revealing hidden genetic variability. The use of a single gravid female to start a culture would greatly simplify interpretation of results, and the use of an artificial diet would permit the maintenance of the culture throughout the year.

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INSTRUCTIONS TO AUTHORS

Manuscript Format: Two copies *must* be submitted (xeroxed or carbon papered), double-spaced, typed, on 8½ x 11 inch paper with wide margins. Number all pages consecutively and put author's name at top right corner of each page. If your typewriter does not have italic type, underline all words where italics are intended. Footnotes, although discouraged, must be typed on a separate sheet. Do not hyphenate words at the right margin. All **measurements** must be metric, with the exception of altitudes and distances which should include metric equivalents in parenthesis. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as example: 4. IV. 1979 (day-arabic numberal; month-Roman numeral; year-arabic numeral). Numerals must be used before measurements (5mm) or otherwise up to number ten e.g. (nine butterflies, 12 moths).

Title Page: All papers must have the title , author's name, author's address, and any titular reference and institutional approval reference, all on a separate title page. A **family citation must** be given in parenthesis (Lepidoptera: Hesperiidae) for referencing.

Abstracts and Short Papers: All papers exceeding two typed pages must be accompanied by an abstract of no more than 300 words. An additional summary is not required.

Name Citations and Systematic Works: The first mention of any organism should include the full scientific name with author (not abbreviated) and year of description. New descriptions should conform to the format: male: female, type data, diagnosis, distribution, discussion. There **must** be conformity to the current International Code of Zoological Nomenclature. We strongly urge deposition of types in major museums, all type depositions must be cited.

References: All citations in the text must be alphabetically listed under Literature Cited in the format given in recent issues. Abbrevations must conform to the *World List of Scientific Periodicals.* Do not underline periodicals. If four or less references are cited, please cite in body of text not in Literature Cited.

Tables: Tables should be minimized. Where used, they should be formulated to a size which will reduce to 4 x 6½ inches. Each table should be prepared as a line drawing or typed with heading and explanation on top and footnotes below. Number with Arabic numerals. Both horizontal and vertical rules may be indicated. Complex tables may be reproduced from typescript.

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Legends should be separately typed on pages entitled "Explanation of Figures". Number legends consecutively with separate paragraph for each page of illustrations. Do not attach to illustrations. Retain original illustrations until paper finally accepted.

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THE JOURNAL OF RESEARCH
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IN THIS ISSUE

COVER ILLUSTRATION: Ventral aspect of stubby-winged mutant of *Limenitis archippus*. See Platt, page 217.

THE JOURNAL OF RESEARCH
ON THE LEPIDOPTERA

STATEMENT OF OWNERSHIP AND MANAGEMENT

Invited Paper

The Phylogeny of Butterflies (Papilionoidea and Hesperioidea)

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Abstract. A phylogenetic tree for butterflies and skippers is derived, using the common possession of derived traits to delimit monophyletic taxa. All available characters of larvae, pupae, adults, and behavior are used, including various new characters. The traits of the progenitor are deduced, and the exact character changes at each point of the tree are specified. The tree accepted is mostly similar to that of Ehrlich. However, within Nymphalidae, Apaturinae is elevated to a subfamily distinct from Charaxinae; and within Lycaenidae, Curetinae is elevated to a subfamily branching from the base of the Riodininae line, and Aphnaeini is elevated to tribal status; Megathyminae clearly belongs to the monocotyledon-feeding branch of Hesperiidae. Most characters support the origin of Pieridae from the Papilionid ancestral line, and the origin of Lycaenidae from the Nymphalid-Libytheid ancestral line. The few characters that seem to have been subject to state reversal, or evolved the same state independently repeatedly, are discussed.

Introduction

This paper attempts to reconstruct the phylogenetic tree for butterflies. The major recent contributor to this subject was Paul R. Ehrlich, who published an intuitive tree based mainly on adult skeletal features (Ehrlich, 1958b) and a computer-analyzed tree based on similarity of various internal and external features of adults (Ehrlich, 1967). Many other authors have contributed studies of various aspects of the subject. Kristensen (1976) published a useful paper using the methods of cladistics, and presented a phylogenetic tree differing in significant features from those of Ehrlich. This paper compiles the available characters from the literature, and interprets them using phylogenetic (cladistic) methods. It includes various new characters, and other characters elucidated by systematically examining all butterfly families for characters previously reported for only one or a few taxa. I also made a special study of first-stage larvae (mainly using chaetotaxy, which will be reported elsewhere in detail) and have included characters of larvae and pupae and behavior which other authors have not used. Questionable characters

were examined (some were found to be useless, see Useless Characters, below).

The phylogenetic (cladistic) principles used are: 1) taxa above the species-level should be defined on the basis of the common possession of unusual derived traits; and 2) each named taxon should have only one root (the taxon should be monophyletic).

The first principle, called by cladists "synapomorphy", or the shared possession of derived ("apomorph") traits, has been used by a few good systematists for centuries. For example, the possession of a larval osmeterium, a unique derived trait, indicates that the family Papilionidae is monophyletic. The presence of special lobes on the prolegs, and of peculiar ant-related glands on larvae of Lycaenidae, suggests the monophyletic nature of taxon Lycaenidae (including Riodininae). Likewise, the common possession of the unique trait of "hindwing rubbing" is enough to set the Theclini-Lycaenini-Polyommatini apart from the rest of the Lycaeninae (though a reviewer states that *Charaxes*, a Charaxine Nymphalid, does this also to draw attention to a false head), while the possession of special lobelike abdomen glands on females of Pierinae-Coliadinae and a special posture for the wafting of the male-repellent scent produced, suggests that this group is a monophyletic entity. In practice, "derived" merely means that the character changed in state, thus in practice various trial trees are drawn with all the character changes placed at their proper points on each tree as indicated by the data, and that tree chosen which minimizes the number of character changes and minimizes the number of absurdities. However, characters that are unique, complex, and highly unusual, such as the evolution of an osmeterium, should be given more weight than common character changes or the mere loss of a structure.

The second principle is more controversial, but I think is gaining acceptance. For instance, it requires the division of the old class Reptilia, because the bird and mammal classes evolved from that omnibus class, making it not monophyletic unless birds and mammals are included in it too. I use these cladistic principles because they seem to be logical, and because Kristensen (1976) claims that cladistics supports a different classification than that of Ehrlich (1958b, 1967). My results, using a larger data set than that of Kristensen, but analyzed with the same principles, are more like those of Ehrlich (1958b), with a few changes in Lycaenidae and Nymphalidae. The trees adopted through intuition and computer-analyzed similarity by Ehrlich do not contradict the present tree.

Fossil Record

The first proto-butterfly apparently evolved in the Cretaceous perhaps 100-80 million years ago (mya), judging from the widespread distribution of the families

and subfamilies (except those with only a few species) in relation to continental drift (South America last touched Africa about 80 mya, Smith et al., 1981), and based on their relationships with flowering plants, which evolved mostly in the Cretaceous. However, butterflies could have evolved somewhat later, perhaps even in the Paleocene, as a few wind-blown adults and various extinctions could have confused the zoogeographic picture; but this is not as likely. The most "primitive" Hesperiidae (many Pyrginae), Papilionidae (Baroniinae), Pieridae (Dismorphiinae plus many Coliadinae), and many Lycaenidae, all feed on Leguminosae, so it is reasonable to assume that the proto-butterfly ate this family. Since the Leguminosae is one of the most "advanced" (derived) families of plants, the ancestral butterfly apparently evolved when the dicotyledons were rather far along in their evolution. However, many fossils of many diverse groups of Leguminosae are known from the early Cretaceous, which is consistent with 100 mya or older. There is uncertainty in time of butterfly origin because, by the time of the first known fossil butterflies, the families were apparently fully evolved. Eocene fossils (48 mya) include several Papilionidae (one like modern *Baronia*, Baroniinae), one Nymphalid (Satyrinae), and one Lycaenid (Riodininae) (Durden & Rose, 1978). Lower Oligocene fossils (38 mya) include Papilionidae, Pieridae, Nymphalidae (Satyrinae, Apaturinae close to modern *Doxocopa*, Nymphalinae close to modern *Hypanartia* and others), Libytheidae (close to modern *Libythea*), Lycaenidae, and Hesperiidae (Scudder, 1889; Brown, 1976; Shields, 1976).

Source of Data

Many of the data are from Ehrlich (1958a, 1958b, 1960, 1961; Ehrlich and Davidson, 1961; Ehrlich and Ehrlich, 1962, 1963), but Kristensen (1976) gives other traits, Brock (1971) a few thorax characters, Petersen (1965) and Fracker (1915) some larval characters, and Mosher (1916) some pupal traits (but see Useless Characters, below). Munroe (1961), Klots (1931), and Eliot (1973) provide useful characters on several families. Other authors provide a few useful traits, as cited below. I have found characters on larvae (especially first-stage larvae—see Hinton, 1946 for terminology—and the larval Lycaenid head), on pupae, the adult wing base, thorax, legs, abdomen base, genitalia, and some characters of larval and adult behavior. A few of the characters have been reinterpreted as noted. Figures 1-2 illustrate structures on the thorax and wing base, because some new characters and names introduced by Brock (1971), Matsuda (1970), and Sharplin (1963a, 1963b) create some confusion that needs clarification by figures. Tables 1 and 2 list the complex characters. To chart the changes of a structure, note its state in "Traits of the Ancestor of Hesperioidea and Papilionoidea" below; then note that the structure retains this state in all taxa unless a change is stated later in the text. Of course, the original references, especially those of Ehrlich, should be consulted for a character also.

Character Enumeration

No phylogenetic tree can be acceptable unless accompanied by precise statements of exactly how each character changed at each point of the tree, documenting the transformation of the ancestral species into the living taxa. Cladistics has been criticized as being merely a classification of characters, but actually the precise listing of character changes at each point of the tree is one of its

strengths. The following is a reconstruction of the ancestor of butterflies and skippers, a justification for the branching sequence, and a listing of how each character changed at each point of the tree of Figure 3 during the evolution of butterfly families, subfamilies, and tribes.

The Moth Progenitor

The closest living relatives of the butterflies and skippers are the other Macrolepidoptera, namely the Sphingoidea, Bombycoidea, Noctuoidea, and Geometroidea (Scott, 1985), rather than the Butterfly Moths, Castniidae. The colorful non-folding wings of Castniidae are evidently a convergent adaptation to diurnal flight. The lack of a jugal fold in Castniidae is because this structure is involved in wing-folding (Sharplin, 1963-64). The Castniid antenna club is shaped like that of skippers, but Jacqueline Miller (pers. comm.) has found that the microscopic details of the antennae are totally different (the Castniid club also has a hairy tip). The paracoxal and marginopleural sulci (Fig. 1) are joined in some Castniidae as in Hesperiidae (Brock, 1971), but their different arrangement in other Castniidae suggests convergence. Likewise the dorsal chamber of the heart of some Cossidae, as in butterflies (Hessel, 1969), has been interpreted as a phylogenetic link, but other Cossids have a looped heart or ventral heart like most primitive Ditrysia, which again indicates convergence, especially as other primitive ditrysians have evolved a looped heart. Miller (1971) found a wide orbit ("eye ring") in Castniidae, nearly as wide as that of skippers, but in skippers this structure is perhaps unique in having tiny ommatidia (Ehrlich, 1960), whereas my examinations show no ommatidia in the orbit of Castniidae, which is similar to that of other moths. Castniidae also share with Megathyminae (Hesperiidae) larvae which bore into monocotyledons; however this must be convergence, because young *Megathymus* larvae make silked-leaf nests as do other skippers. First-stage Megathyminae larvae share many derived traits with Hesperiinae, notably a lack of the second SD seta on thorax segments 2-3 of first instars.

Traits of the Ancestor of Hesperioidea and Papilionoidea

This ancestor had a large non-foldable hindwing, and apparently lost the spine (frenulum) and catch (retinaculum) that hook moth wings together. Only *Euschemon* (Hesperiidae, Pyrginae) has a frenulum and retinaculum today. This trait needs discussion because it does not seem to obey any usual evolutionary principle. If we assume that, once lost, these parts cannot be regained, then, because *Euschemon* is otherwise a normal member of the Pyrginae (Evans, 1949), these parts must have been lost independently at least four and up to a dozen or more times (by the Hesperiinae-Megathyminae ancestor, by the ancestor of Pyrrhopyginae, by the remaining Pyrginae, and by the ancestor of Papilionoidea). A more likely explanation is that a regulatory gene controlling the development of the frenulum and retinaculum lost its function through a mutation in the ancestor of all butterflies and skippers, and that after *Euschemon* evolved, a reverse mutation restored the function of the gene, activating the dormant frenulum-retinaculum genes. (A virus-transferred gene could have had the same result.) Forbes (1960) suggests that a tuft of setae at the end of a short thickening of the costa in Riodininae replaces a frenulum, perhaps a less-perfect reappearance of a similar origin.

Table 1. Character states among the families. a = absent; p = present; s = present but small; l = large; capitalized letters are derived states, uncapitalized letters are primitive stages; Macro = Macrolepidoptera.

Character	Pap	Pier	Nym	Lib	Lyc	Hesp	Macro
1st stage larval annuli	a	a	a	a	P	P	a
#L setae 1st stage prothorax	2	1(2)	2	2	2	2	2
ventral neck gland larva	A	pA	pA	pA	A	pA	aP
osmeterium	P	a	a	a	a	a	a
crochets in circle mature larva	a(P)	a	a	a(S)	a	P	a
lateral crochets mature larva	A(S)	A	A	S	A(S)	p	p
pupa attached by cremaster	p	p	p	p	pA	p	p
pupa attached by silk girdle	p	p	A	A	p(A)	p	?
temporal cleavage line pupa	A	A	A	A	A	p	p
antenna hooked	A	A	A	A	A	p	ap
antenna cleaning (e=epiphysis, F=femur tuft, T=tibia brush	e	A	FT	FT	FT	e	e
tiny ommatidia in eye orbit	a	a	a	a	a	P	a
retina cells cross (x) or rosette (r) shaped	x	x	r	r	r	?	?
fw R veins branched	P	P	P	P	PA	a	ap
fw vein 2A joins 1A	A	p	p	p	p	p	p
2nd median plate fw base	A	p	p	p	p	p	p
male forelegs	l	l	S	P	S(L)	l	l
pulvilli (f=forked; s=single)	A	S(A)	f(A)	f	S	f	f
tiny dorsal tarsal spines	P	P	a(P)	a	a(P)	a	a
spurs middle leg tibia	A	p	p	p	p	A	p
upper pair spurs hindleg tibia	A	A	A	A	A	p	p
antenna cleaning by foreleg (f) or middle leg (m)	f	f	M	M?	M	f	f
cervical sclerites united	P	a	a	a	a	a	a
prothorax presternum	A	A	p	p	p	p	p
anterior rim T1 spiracle adult	S	S	S	S	S	p	p
paracoxal sulcus joins marginopleural	P	P	P	P	P	a	a
meral sulcus metathorax	P	a	a	a	a	a	a
scutum 3 view from rear	S	S	L	L	L	p	p
prespiracular bar	p	A	p	p	p	p	p
postspiracular bar	a	P	aP	L	a	aP	a
horizontal chamber aorta	A	p	p	p	p	p	p
secondary sternopleural sulcus	A	A	L	S	L	S	a

Table 2. Character states among the subfamilies. Symbols are the same as in Table 1.

Character	Macro	Pyrth	Coel	Pyrg	Trap	Hesp	Mega	Lyc	Curet	Riod	Styg	Libyth	Calin	Acrae	Nymph	Apat	Char	Morph	Satyr	Ithom	Dan	Pier	Col	Disin	Pseud	Baron	Parn	Papil
secondary setae 1st instar	aP	a	a	a	a	a	a	p	p	p	—	a	—	a	aP	a	aP	aP	a	P	P	a	a	a	a	P	P	P
#SD setae on mesothorax 1st instar	2	2	—	2	—	1	1	0-3	7	3	—	1	—	2	2,5	2	2	2	2,1	—	2	2	2	1	—	6	4	5
#SD setae on metathorax 1st instar	2	2	—	2	—	1	1	0-3	8	3	—	1	—	2	2,5	2	2	2	2,1	—	2	1	1	1	—	6	4	5
larval body scoli	aP	2	—	2	—	1	1	a	a	aP	a	1	a	2	P	a	2	a	a	a	2	a	1	1	a	6	a	aP
pupal middle leg touches eye	a	a	a	a	a	a	a	a	a	a	a	a	a	P	a	a	a	a	a	a	a	a	a	a	a	a	a	a
antenna scaled	a	a	a	a	a	a	a	a	P	a	a	P	P	P	P	P	P	P	P	P	P	p	p	p	p	p	pA	A
hw vein 3A	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	A	A	A	A	A	S	A	S
patagia	p	p	p	p	p	p	p	A	A	A	A	S	1	1	1	1	1	1	1	A	A	A	p	A	A	S	S	S
parapatagia	1	1	1	1	1	1	1	A	A	A	A	A	A	1	1	A	S	A	A	A	A	A	A	A	A	A	A	A
anepisternum mesothorax	1	1	1	1	1	1	1	AS	1	1	1	A	1	A	A	A	1	1	S	A	A	A	A	A	A	1	lS	lS
mesodiscrimen curved down to base of furca (a), partly curved (s), or extending straight back to furca (l)	a	a	a	a	a	a	a	A	A	A	A	L	L	L	L	L	L	L	L	L	L	L	L	L	L	S	L	L
adult peritrophic membrane from front of midgut (f) or de-laminated from midgut epithelium (e)	f	—	—	e	e	e	—	f		—	—	—	—	—	e	—	e	—	e	—	f	f	f	—	—	—	—	f

Fig. 1.   Adult thorax, lateral view. Some terms in Figs. 1-2 differ from those of other authors, due to the work of Matsuda (1970), Sharplin (1963a, 1963b), and Brock (1971). When no clear-cut choice of terms was found, those of Matsuda were used, because his book covers all insects.

The wing veins of the ancestor resembled those of modern skippers (with no areole), except the hindwing discal cell was closed by a vein at its end, and hw vein M_2 was present. In the pupal forewing, R_{4-5} branched from the radius basad of R_1 and R_{2-3} (Headlee, 1907; Zeuner, 1943; Tindale, 1980). The ability to roof the wings over the abdomen was lost. Wing base structures were like those of other Macrolepidoptera such as Noctuidae (Sharplin, 1964). The antennae were clubbed, probably as in modern Papilionidae and Lycaenidae, or, farther back in time, as in some Sphingidae. The head lacked the two dorsal ocelli of most moths, but possessed chaetosemata. Adults were day fliers, and had large optic lobes of the brain for better vision. The head had paratemporal sulci (the temporal sulci of Miller, 1971) which are relatively unchanged in Hesperiidae and Papilionoidea. The temporal cleavage line of the pupa ("epicranial suture" of Mosher, 1916) was present, and is represented in adults by the "transverse suture" of Miller (1971), which I am calling the temporal sulcus. The temporal sulcus of adult Papilionoidea (Ehrlich, 1958a) is probably homologous with Miller's "transverse suture" in Hesperiidae, and has assumed a different course (parallel to the paratemporal sulcus) because the Papilionoid pupa lacks a temporal cleavage line (the position of the temporal sulcus in adult *Lycaena*, see Ehrlich 1958b, is perhaps primitive). The head had a distal transoccipital band and the laterofacial sulcus was lateral to the tentorial pits, as in Hesperiidae (Miller, 1971). The foreleg had an epiphysis but no tibial spurs, the middle legs had two spurs, the hindlegs four. The pulvilli on the legs were forked; tiny dorsal spines were absent on the tarsi, but hairlike bristles were present above the claws. The aorta had an enlarged horizontal chamber with two lateral ostia in the mesothorax. The midgut was probably shaped like that of Hesperiidae (Homma, 1954). On the thorax the presternum was present, the patagia and parapatagia were sclerotized, the first spiracle had a strong rim all around it, the paracoxal ("precoxal" of Brock, 1971) sulcus was not membranous and was directed anteriorly and not fused with the marginopleural sulcus, on the mesothorax the hypopteral sulcus (derived partly from the parepisternal sulcus of Brock, 1971) completely circled a hypopteron, the upper sector of the paracoxal sulcus (precoxal sulcus of Brock, 1971; see origin of Pieridae below) was lost, the secondary sternopleural sulcus developed, the anapleural cleft was fused together, and a postcoxal sclerite was on the top rear of the mesothorax meron. A muscle from the mesoscutellum to the mesopostnotum (pterothorax character #7 of Ehlrich and Ehrlich, 1963) was twisted, which Kristensen (1976) states is a derived feature of skippers and butterflies (except Lycaenids now have the muscle untwisted). Scutum 3 was visible somewhat from the rear, and a muscle from scutum 3 to the third phragma (pterothorax character #13 of Ehrlich and Ehrlich, 1963) was fanshaped. The mesothorax discrimen curved down to the furca base as in the metathorax, and the secondary furca arms in the metathorax were fused together for a short distance. The peritrophic membrane was apparently formed at the front of the adult midgut (Waterhouse, 1953). The transphragma between thorax and abdomen had two internal laminae (Brock, 1971). The anterolateral apodemes on the first abdomen sternite (sternum 2) became very small (tiny but present in all six families), a unique trait among Ditrysian Lepidoptera (except for some Limacodidae, Brock, 1971). Sternum 2 on the abdomen had a long anterolateral projection to the thorax and tergum 1 (the prespiracular bar). (Another character, the postspiracular bar, was possibly present also, but is functionally related to the

prespiracular bar, so if one is present the other is usually absent. It is complete only in Pieridae, a few Nymphalidae, Libytheidae, and a few Hesperiidae such as *Capila* but not *Epargyreus*.) The pupa had clubbed antennae, and a temporal cleavage line between antenna bases ("epicranial suture" of Mosher, 1916), maxillary palpi were absent, the mandible remnants ("pilifers" of Mosher, 1916) were usually close together or touching, the femur was not visible on the foreleg, and the abdomen had only weak setae (no spines) and was movable only at joints 4-5, 5-6, and 6-7. The pupa lacked a silk cocoon, and was attached by both the cremaster and a silk girdle. The larvae ate leaves of dicotyledon plants, probably Leguminosae. Mature larvae had hundreds of short secondary setae, and the crochets were in three lengths (triordinal), in one row (uniserial), in a circle or (probably) inner semicircle. But first stage larvae had only "primary setae" (see Hinton, 1946 for names of these), including one SV and two SD setae on the meso- and metathorax, one L seta on abdomen segment 9, setae L1 and L2 were far apart on abdomen segments 1-8, and the crochets were probably in a circle. The postnatal ("subprimary") seta L3 was absent on the prothorax of second-stage larvae (secondary setae obscure its absence in older larvae). Proprioceptor seta MXD1 may have been absent on the prothorax, as it is absent in the few living taxa checked (*Pieris*, Hinton, 1946; apparently *Everes*, and *Lycaena*, Wright, 1983). The older larva had a ventral neck gland, now present in Hesperiidae (Hesperiinae at least), Pieridae (Dismorphiinae, Pierinae, and Coliadinae at least), Nymphalidae (Danainae, Morphinae including *Caligo*, Nymphalinae at least), and Libytheidae, and eggs were upright, both traits as in Noctuoidea.

Family Branching Sequence

Before proceeding to the butterfly phylogenetic tree and detailed enumeration of associated character changes, justification for the sequences of branches must be given. For this analysis, we can start with a partial tree, with Hesperiidae branching from the base, and the tree then forking into Papilionidae and Nymphalidae-Libytheidae. Virtually everyone who has ever written on butterfly phylogeny has accepted this partial tree. The points of origin of Pieridae and of Lycaenidae must now be ascertained on this partial tree.

Origin of Pieridae

Ehrlich (1958b) found that Pieridae are most similar to Papilionidae morphologically. But Kristensen's (1976) cladistic analysis placed the origin of Pieridae from the stem of Nymphalidae-Lycaenidae rather than the stem of Papilionidae. The following characters (denoted by small letters) support the origin of Pieridae from the Papilionid line: the secondary sternopleural sulcus (sss) (of Brock, 1971; =precoxal suture of Ehrlich, 1958b) (Fig. 1) is weakly developed in skippers (Kristensen, 1976 discards this character because he and Brock did not realize that it is present in skippers; my dissections show it in *Erynnis, Epargyreus*, etc.). Brock illustrates it in skippers and labels it the "upper sector of the precoxal suture", which is a misinterpretation, as this sulcus ("suture") arises from the rear of the anapleural cleft in all moths. Phylogenetically, the upper sector of the paracoxal ("precoxal") sulcus very doubtfully crept down the pleural sulcus to form the sss, because the pleural sulcus is an internal strengthening ridge and does not need the assistance of such a creeping rudiment. In skippers the sss strengthens the ventral

edge of a slight dome in the episternum. The sss seems homologous in Hesp.-Nym.-Lyc. (Hesperiidae-Nymphalidae-Lycaenidae). The secondary sss has (a) become lost in Pier.-Pap. (Pieridae-Papilionidae), but (b) in Nym.-Lib. (Libytheidae)-Lyc. it is strongly developed and usually also runs behind the pleural sulcus, (c) forming an area called the preepimeron (present in Nymphalidae and Lycaenidae).

In skippers, scutum 3 is somewhat visible from the rear, but (d) in Pap.-Pier. (Papilionidae-Pieridae) scutum 3 is scarcely visible from the rear, and (e) in Nym.-Lib.-Lyc. scutum 3 is very visible from the rear. These shape differences may have affected (or resulted from) flight behavior: most of the Pap.-Pier. patrol to locate mates, whereas many of the Nym.-Lib.-Lyc. perch (Scott, 1975). (f) The prothorax presternum is absent in Pap.-Pier. but present in Nym.-Lib.-Lyc. (and seems to occur in Hesperiidae). Several weak characters, internal prothorax structures, are similar in most Pap.-Pier.: (g) the furcal arms have a secondary anterior lamella or prong (absent in *Baronia*), (h) the intercoxal lamella has migrated back to the furca (see Ehrlich, 1958b, Figs. 29, 30) except in *Baronia*, and (i) the discrimen generally (but not in Baroniinae or Parnassiinae) has an anterior spine or lamella. (j) The retina cells are cross-shaped in cross-section in Pap.-Pier., but rosette-shaped in other butterflies (Yagi and Koyama, 1963). (k) The radial plate on the forewing base seems to be hardened posteriorly in the same manner in Pap.-Pier. (1) The spinasternum is expanded laterally in front of the spina in Pieridae and most Papilionidae (but this is a weak character, as *Baronia* (Pap.) lacks the expansion, and in Pieridae the expansion is much less, see Ehrlich, 1958b). (m) The labial sclerite is often membranous in Pap.-Pier., sclerotized in Nym.-Lib.-Lyc. (however it is membranous in front of the palpal sockets in Pap., behind them in Pier. The primitive state may be membranous as in most *Hesperiidae* (Miller, 1971), in which case the membranous labial sclerite of Pap.-Pier. and Styginae may be primitive as well). (n) The female has a cover-flap over the mating tube in Pap.-Pier., which I have not seen in other families (however this is another weak trait, as the flap is now limited to Papilioninae, Pierinae, and Coliadinae). (o) A frontoclypeus-proboscis muscle is present in some skippers and in Pap.-Pier., but is absent in Nym.-Lib.-Lyc. (character 3 of Ehrlich and Ehrlich, 1962). (p) The male forelegs are normal size and fully functional in Pap.-Pier., smaller in Nym.-Lib.-Lyc. Antennal cleaning is done by the middle legs of both sexes of Nymphalidae and Lycaenidae, but by the forelegs of Pap.-Pier.-Hesp. (Hesperidae) (Jander, 1966). (The epiphysis of Pap.-Hesp. is an antenna-cleaning device. Another such device developed by Lycaenidae is a scale tuft on the mesothorax femur and an opposable grooved scale brush on the tibia, which remove debris as the antenna is passed through the flexed leg; Libytheidae have a strong femur tuft but it is small in Nymphalidae, and both families plus some Riodininae have a weak or absent tibial brush.) Jander found that even the Lycaenidae with large forelegs use the middle leg for cleaning, which proves that the ancestor of Lyc.-Lib.-Nym. had a small foreleg and thus developed middle-leg cleaning. Detection of sugar for feeding is by the forelegs of Pieridae (and undoubtedly Papilionidae), but by the middle legs of Nymphalidae (and presumably Lib. and Lyc.) (Frings & Frings, 1956). (q) The tiny spines all along the top of the tarsi are present in Pap.-Pier., but absent in Castniidae, Hesperiidae and Nymphalidae (except for *Dioriste*, Satyrinae, an unusual convergence, and the fine dorsal spines of Ithomiinae, Forbes, 1939)—Lib.-Lyc. (except for *Iraota* and *Amblypodia*,

Lycaeninae, also convergence). Kristensen (1976) cites this as a derived trait of Nym.-Lyc., but actually it is a derived trait of Pap.-Pier., and spines are absent in moths and skippers. (r) The eyes are hairy in many Nymphalidae and Lycaenidae, bald in Pap.(except *Bhutanitis mansfieldi*)-Pier., a weak character. (s) The papillae on the tip of the proboscis (taste organs) tend to be larger in Nym.-Lib.-Lyc. than in Pap.-Pier. (Ehrlich, 1958b), but this seems to be a weak character owing to variation among genera. (t) Forewing vein M_2 is close to M_3 (a "quadrific cubitus") in Papilionidae and some Pieridae (Dismorphiinae), and Klots (1931) suggested that this venation is primitive in Pieridae. This seems to be a weak trait, as the other Pierid subfamilies differ, and have a more Nymphalid-like venation. (u) The spinasternum is much more heavily sclerotized between its two main points of attachment to the mesothorax in Pap.-Pier. than in other families. Pupae of Papilioninae and Pierinae commonly have both green and brown forms, but this may be convergence (*Nymphalis urticae*, Nymphalidae, also has these forms).

The following characters support the origin of Pieridae from the Nymphalid-Libytheid line: (v) A prothorax muscle from the spinasternum to the coxa (character 11 of Ehrlich & Ehrlich, 1963) is present in Hesp.-Pap., but lost in the others. (w) The epiphysis is present in Hesp.-Pap., but lost in the others. (x) The antenna club is pendulum-shaped in many Pier.-Nym.-Lib. (a very weak character that undoubtedly arose independently, as many other genera of Pier.-Nym. have rodlike clubs). (y) The maxillary palp is one-segmented or absent in Hesp.-most Pap.-Pier.-Nym.-Lyc., and two-segmented in one Papilionid genus (*Baronia*). Kristensen placed this character here, but it seems very weak, because it is one-segmented in Hesperiidae. *Baronia* probably reacquired a two-segmented rudiment. (z) In Noctuidae, Hesperiidae, and Papilionidae the papilla analis apophysis retractor is attached to segment 7, but in Pier.-Nym.-Lyc. it has shifted to segment 8 (Stekol'nikov, 1967; though the tree adopted by Stekol'nikov is identical to that of Fig. 3). Brock (1971) stated that Pier.-Nym.-Lyc. have a wide secondary sclerite on the metathorax scutellum, and Kristensen cited the character here. However, I dissected examples of every family and could not find this structure, nor did Ehrlich find it; it is not defined by either membranous boundaries or by internal ridges (sulci). Chapman (1895) stated that the pupal abdomen of Pier.-Nym. moves only laterally, whereas the abdomen of Hesp.-Pap. can move in all directions; this seems a very weak character, as the *Papilio* abdomen seems rather rigid, moving only at joint 4-5 (weakly at 5-6), and the *Papilio (brevicauda)* pupae I disturbed wiggled the abdomen only laterally.

If the weak characters are given half a point and others one point (although character p may represent three characters), then 17½ characters support the origin of Pieridae from the Papilionid line and only three support its origin from the Nymphalid-Libytheid line. Some of these characters represent loss of a trait rather than a new development, and it is generally much easier to lose a trait than to originate it. A taxon is probably monophyletic if it has some unusual derived traits. Pap.-Pier. has many traits that may qualify (g, h, i, j, k, l, n, q, t and u—some of these are weak characters), and Nym.-Lib.-Lyc. has some strong characters (b, p, r, s), whereas the Pier.-Nym.-Lib.-Lyc. has no strong characters. The few characters supporting the latter grouping represent losses of structures, or are weak.

Origin of Lycaenidae

Lycaenidae undoubtedly arose from the Nym.-Lib. ancestral line. Eight charac-

ters support this origin of Lycaenidae (b, c, e, f, o, p, q, r, s—the last two are weak traits each counted ½). Four traits support the origin of Lycaenidae from the stem of Papilionoidea before the Papilionidae and Nymphalidae ancestors diverged: (A) A metathorax muscle is fan-shaped in skippers and Lycaenidae, but more parallel-sided in all other families (pterothorax character #13 of Ehrlich & Ehrlich, 1963). Evidently the Pap.-Pier. and Nym.-Lib. ancestors independently developed a parallel-sided muscle. (B) First-stage larvae of skippers and Lycaenidae have annuli (chitin rings), which other families lack. These annuli may be glands in Lycaenidae (Wright, 1983 notes perforations in the dome-shaped top of the cone-shaped ring of the annulus "lenticle" of *Lycaena* third and fourth instars—are annuli related to the "perforated cupolas" of Malicky, 1970?), are doubtfully vestiges of lost setae, and apparently evolved independently. (C) The mesothorax discrimen dips down to the base of the furca in skippers and Lycaenids, but extends straight back to the furca in all other butterflies (except it curves slightly down in *Baronia*). The metathorax discrimen dips to the furca base in all skippers and nearly all butterflies (except *Pseudopontia*), so the Lycaenids may have regained the ancestral form by using metathorax genes. (D) Chapman (1895) notes that pupal setae are prominent on Hesp.-Lyc., absent or small on Pap.-Pier.-Nym. (though minute in some such as *Limenitis*); no doubt the setae were generally lost in the latter groups, which are more exposed and colorful (Nymphalinae and Acraeinae pupae have various cones or scoli, of course). Only one trait supports the origin of Lycaenidae from the Pap.-Pier. ancestral line: (E) pulvilli are single in Lyc.-Pier. (absent in Papilionidae), but forked in all other families, which undoubtedly represents independently derived states of fusion of the forks.

Evolution of Skippers (Hesperioidea)

Skippers were the first group to split off of the butterfly line (Fig. 3), probably in the Cretaceous period. Skippers kept most of the traits of the butterfly-skipper ancestor (but at least some other butterflies lost some of them). After skippers branched from the line leading to Papilionoidea, they evolved some new traits. The hindwing discocellular veins were largely lost in skippers, and vein M_2 became weak or absent. The humeral vein became pointed toward the wing base, and the wing edge (costa) thickened at the base. A stigma may have occurred on the male forewing, as a discal stigma is present in Coeliadinae, Hesperiinae, and "Trapezitinae." The antenna club of skippers is perhaps a modification of the enlarged and hooked antenna found in most Sphingidae; if not, the ancestral skipper must have developed a bent club as in Pyrginae, and the Hesperiinae and other clubs are modifications. An "eyelash" of scales on the base of the antenna developed in at least some skippers. The orbit of the eye became wider, and developed (functional?) tiny ommatidia (Ehrlich, 1960), perhaps a unique trait in Lepidoptera. The skipper head became very wide. One could hypothesize that the wide head and the rudimentary ommatidia in the orbit are due to a nocturnal butterfly ancestor becoming diurnal. In moths, newly arisen diurnal species evolved a smaller eye (rudimentary ommatidia being a transition stage?) and a wider face (Ferguson, 1971 p. 9-10); however, Ferguson notes that this apparently happens quickly, even between closely related species, whereas skippers have had much more than 50 million years to improve their eye. Horridge (1975) found that the skipper eye has a clear zone between the lens system and retina and truly focuses

light, as in many nocturnal moths, and skippers share with Bombycoidea retinula cell extensions to the lens system, and skippers share with Agaristinae (Noctuidae) an absence of pigment in the clear zone in the daytime. Because Agaristinae and some Bombycoidea are diurnal, a nocturnal butterfly ancestor is not required, and, based on Horridge, the rudimentary lenses in the skipper orbit would help focus the eye at its periphery (Papilionoidea lack a clear zone and do not have focused eyes).

Patches of sense-hairs (chaetosema) often developed on front as well as the rear of the head (Jordan, 1923; only the rear patches are in other butterflies, except *Phoebis*). The spurs on the middle leg tibia were lost (and the upper spurs on the hind leg tibia were later lost in some skippers). The tergal bar connecting the abdomen to the thorax is derived from tergum 1, but it became fused to tergum 2 (with no gap or sulcus at the point of fusion, a trait unique or nearly so). The adult peritrophic membrane delaminated from the midgut epithelium instead of the front of the midgut (Waterhouse, 1953). The larvae developed the habit of living in a leaf rolled and silked into a tube, which provided the selective basis for developing (or perhaps retaining) crochets in a complete circle in mature larvae (because the outer crochets can grip the nest). The larval neck became narrow (except in Giant Skippers), to allow the head to swing about inside the leaf nest to silk it into a tube. Some pupae are suspended inside the larval leaf nest by a Y-shaped silk girdle (the cremaster is not attached strongly). As other adaptations to this habit, the larvae seldom wander like other butterflies before pupation, and the mature larvae developed powder glands beneath abdomen segments 7 and 8 to provide water repellent powder for the pupa in the nest. First-stage larvae developed hardened rings (annuli) on the body, which may be glands; they have only primary setae, which are usually enlarged or forked at the tip. Older larvae have only short setae, and have no spines or antlers, although some Hesperiinae have conelike horns and two fleshy tails.

Early in their evolution, skippers split into two groups. This basic division is obvious, but the remaining evolution of skippers is rather obscure (see Miller, 1971). The first group switched to monocotyledons (grasses, etc.) for food, the antenna club stayed oval with a small pointed tip, a peculiar unique basking posture evolved (the hindwings are spread much more than the forewings), the base of forewing veing M_2 moved closer to vein M_3 than to M_1 (it varies in "Trapezitinae"), and first stage larvae lost the second SD seta on thorax segments 2-3. This ancestor produced the Megathyminae, which are borers in Agavaceae, and the Hesperiinae. The Megathyminae adult head became smaller, the larval prothorax became wider, the first stage larval hairs grew longer, and the plateau behind the thorax spiracle on the pupa disappeared. I include the Trapezitinae in the Hesperiinae because, based on Evans' (1949) findings, it seems unlikely that Hesperiinae is a monophyletic group if Trapezitinae is excluded from it. Trapezitinae are weakly characterized by having the end of the hindwing discal cell sloping toward the body. Megathyminae have often been treated as a distinct family, but there is no doubt that they evolved from this monocotyledon branch of skippers. Furthermore, it is possible that they too are merely an unusual offshoot of Hesperiinae, cladistically. Within Hesperiinae, the *Carterocephalus* (America-Eurasia)-*Heteropterus* (Eurasia)-*Astictopterus* (Africa) group of Evans (1937-1955) may be the most distinct group.

The second group of skippers ate dicotyledons (some *Urbanus* later switched to monocotyledons), the antenna club became mostly boomerang-shaped, and the base of forewing vein M_2 was the same distince to vein M_3 as to M_1. The male hindleg tibia developed a hair pencil that fits between the abdomen and a posterior extension of the metepimeron (this extension a mere long scale tuft in Celaenorrhinus), traits now present in Pyrginae and Coeliadinae. Pyrginae often have characteristic sex glands (a male costal fold, female glands on top of abdomen segment 7, and female abdominal hair pencils). Coeliadinae have the second palp segment stout and erect, the third segment long and projecting forward; the antenna is Pyrginae-like. Pyrrhopyginae developed a shortened abdomen, a more triangular hindwing, an antenna having most of the club beyond the elbow, a very long forewing discal cell, and apparently lost the hind leg hair pencil (or never had it). Whether these three subfamilies are really monophyletic entities remains to be seen. Pyrrhopyginae is probably monophyletic, but it and Coeliadinae are probably just two of the many branches of Pyrginae if principle #2 above is applied. W. Evans (1951-1955) suggests that the ancestor of Pyrrhopyginae and Coeliadinae occurred throughout the tropics when Africa and South America still touched, but when they split the American population became Pyrrhopyginae and the Old World population became Coeliadinae. However, de Jong (1983) states that Coeliadinae and Pyrrhopyginae are not phylogenetically related. de Jong (1975) also shows that the *Telemiades* and *Erynnis* Pyrgine groups of Evans are really just one group.

Unfortunately there is no adequate tribal classification of skippers, and new characters are needed, as the current classification relies too heavily on antennae and palpi.

Evolution of the Ancestor of Papilionoidea

The branch producing the Papilionoidea after the Hesperiidae branched off (Fig. 3) lacked the specialized traits of skippers such as larval powder glands and leaf nest building, and the mature larva wandered before pupating. This branch changed to some extent before splitting. The forewing R veins began to join with each other. (The frenulum and retinaculum were apparently lost earlier, by the ancestor of skippers and Papilionoidea.) The antenna club remained straight, but any angled tip present on the Papilionoidea-Hesperioidea progenitor was lost. The internal structure of the compound eye changed slightly (Yagi, 1953). The orbit of the eye shrank to (or had) a narrow rim lacking ommatidia, extensions of the rhabdoms and pigment ran through the clear zone of the focused skipper eye, the eye shrank on the back of the head, and the transoccipital band seems to have moved more mesally. The temporal sulcus on the head (apparently homologous to the temporal ["epicranial"] cleavage line of Hesperiidae pupae and the temporal sulcus, or "transverse suture" of Miller, 1971, in the Hesperiid adult) changed course (often parallel to the paratemporal sulcus, but perhaps the position in *Lycaena* is primitive). A "laterofacial sulcus" no longer ran ventrally from the frontogenal sulcus as it does in Hesperiidae and various moths including Castniidae. The front rim of the first adult thorax spiracle became mostly desclerotized. The upper pair of spurs of the hindleg tibia was lost, leaving the lower pair on the hindleg and middle leg. On the prothorax the parapatagia became membranous, and the lateral plates of the pronotum developed a Y-shaped structure where they join dorsally.

On the mesothorax the paracoxal sulcus joined the marginopleural sulcus (Fig. 1) (in Hesperiidae they rarely touch in some genera such as *Capila* but are not fused into one sulcus) (in Curetinae, Lycaenidae, a sulcus extending dorsally from the marginopleural resembles the paracoxal sulcus of skippers but is undoubtedly independently derived). The mesothorax anepisternum became small and the hypopteron extended upward farther, and the postcoxal sclerite on the meron moved to the rear. In the mesothorax the discrimen grew straight back to the furca. The metathorax phragma grew larger (later developing stalks or lobes), and the transphragma lost the two laminae of Castniidae and skippers. The posterior ventral lamina (of Brock, 1971) on the metathorax furca disappeared (among Hesperiidae it is small in *Agathymus* and large in *Epargyreus*, extending to the foot, but is not discernible in Papilionoidea). On the front of the midgut the cardia became obvious externally (Homma, 1954). On older larvae the crochets were lost (or, probably, were never present) on the outside of the prolegs (the few outer crochets in Riodininae and Libytheidae and the *Papilio troilus* group at first seem to be rudiments of the ancestral circle, but may be new developments, as young larvae have them, and the Macrolepidopteran butterfly ancestor may have lacked them in older larvae). Mosher (1916) suggested that Hesperioidea pupae might have dorsal movement between abdomen segments 3-4 unlike Papilionoidea, but this is doubtful (not true in pupae I have examined), and the wingtips cover segment 4 ventrally in both groups so any movement of segment 4 is doubtful. The pupa lost the temporal cleavage line between the antenna bases ("epicranial suture" of Mosher, 1916; she listed it in Lycaenidae where it is actually absent, as I cannot detect it). (In skippers the temporal cleavage line is obvious, and each vertex half (on the head) behind the cleavage line remains attached to its thorax pronotum half after adult emergence. Furthermore, the skipper eye-pieces remain attached to the gena of the head, which in turn remains loosely attached to the base of the proboscis (galeae), contrary to Brock, 1971, p. 93.)

The Evolutionary Origin of the Five Families of Papilionoidea

At this point, the Papilionoidea line split in two (Fig. 3). The line leading to Papilionidae and Pieridae developed large wings compared to the body (perhaps contributing to the trend that males of most species of these families patrol to find females, Scott, 1975). The metathorax changed in shape so that the scutum is only slightly visible from the rear (which perhaps altered their flight, also favoring their patrolling behavior). The forewing vein M_2 was apparently close to vein M_3 (a "quadrifid cubitus", primitive in Pieridae according to Klots, 1931, although most subfamilies lack this trait). The radial plate on the forewing base (Fig. 2) became hardened on the rear in the same way. The retina cells of the compound eye became cross-shaped at each level (Yagi and Koyama, 1963). The tarsi developed several rows of dorsal spines (all butterflies have ventral spines). On the prothorax the presternum was lost, the internal keel (discrimen) developed an anterior spine or ridge, and the keel migrated back to the furca, and the arms of the furca also developed an anterior ridge or prong. The spinasternum became much more heavily sclerotized between its two main points of attachment to the mesothorax than in any other family. On the mesothorax the secondary sternopleural sulcus disappeared. The internal muscle connecting the metathorax scutum to the phragma in front of the abdomen became more rodlike (pterothorax character #13 of Ehrlich and Ehrlich, 1963). Abdomen tergites 2-3 possibly lost some movement between

them (tergites 1-2 are always fused in Hesperioidea and Papilionoidea) though this trait is doubtful because *Parnassius* has complete movement. A cover flap apparently developed above the female's mating tube or developed later (it is present in Papilioninae, Pierinae, and Coliadinae). Larvae probably ate Leguminosae.

This phyletic line then split into the Papilionidae and Pieridae ancestors (see below).

The ancestral line leading to Nymphalidae, Libytheidae, and Lycaenidae (Fig. 3) kept smaller wings in relation to the body for more maneuverability, so, as in skippers, males of many species perch to find females (Scott, 1975). The metathorax changed in shape so the scutum became very visible from the rear, which may have contributed to their perching behavior. The eyes probably became hairy, as many Nymphalidae and Lycaenidae have hairy eyes. A muscle from the proboscis to the frontoclypeus was lost (character 3 of Ehrlich and Ehrlich, 1962). The male forelegs became small and nearly useless (some Lycaenidae later reacquired larger segmented and clawed male forelegs perhaps by using female or mesothorax genes, see Lycaenidae); Jander (1966) found that the middle legs clean the antennae in both sexes of Nymphalidae and Lycaenidae, and Frings and Frings (1956) found that the middle and hind legs detect sugar in Nymphalidae (the front and middle legs detect it in Pieridae). The middle leg apparently developed an opposable femur tuft and weak tibial brush for antenna cleaning (both structures were later lost in some Riodininae and a few Lycaeninae, and in Nymphalidae the femur tuft is weak and the tibial brush absent or very weak). The epiphysis on the foreleg was lost. On the prothorax, a muscle from the spinasternum to the leg coxa was lost (prothorax character #11 of Ehrlich and Ehrlich, 1963). On the mesothorax the secondary sternopleural sulcus (Fig. 1) became well developed, and part of this sulcus developed behind the pleural sulcus, forming a space called the preepimeron. The papilla analis apophysis retractor shifted from segment 7 to 8 (Stekol'nikov, 1967).

At this point in evolution, the Lycaenidae probably branched off (Fig. 3, see Lycaenidae below).

The line leading to Nymphalidae and Libytheidae (Fig. 3) underwent further changes. The antennae developed three ventral ridges (these and other butterflies have antennal grooves, but other families lack the ridges), and the antenna often became pendulum-shaped. Inside the head a third muscle developed from the sucking pump to the antenna ridge (character #12 of Ehrlich and Ehrlich, 1962; these muscles vary and some Nymphalidae have lost one or two of the three). The male forelegs became very small. Two muscles from the head tentorium to the cervical sclerite became distinctly separated (prothorax character #2 of Ehrlich and Ehrlich, 1963). A muscle from the metathorax scutum to the phragma in front of the abdomen became more rodlike (pterothorax character #13 of Ehrlich and Ehrlich, 1963). The silk girdle around the pupa was lost, and the pupa now hung only from the cremaster. The visible legs on the pupa all touched the eye. The pupal thorax spiracle changed into a slit.

Now the Libytheidae split off into a separate line, and the Nymphalidae evolved further (Fig. 3; see those families below). Kristensen (1976) suggests, without evidence, that Libytheidae evolved from one of the subfamilies of Nymphalidae, and so should be included in Nymphalidae. However, larval traits suggest that Libytheidae evolved first, and kept an ancestral type of larva, while the
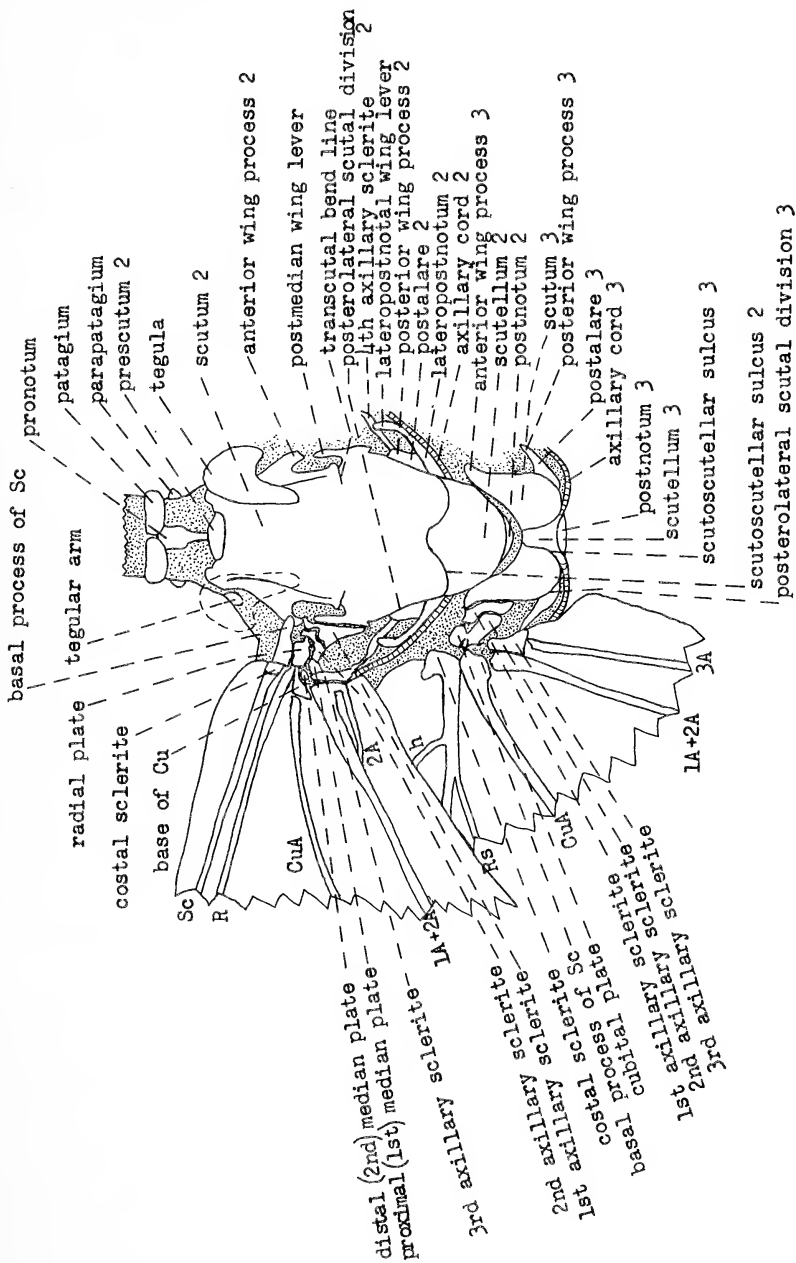
Fig. 2. Adult thorax, dorsal view. See comments in explanation of Fig. 1.

Nymphalidae then evolved small adult female forelegs, and evolved numerous larval spines, antlers, filaments, and tails. The trend in Nymphalidae larvae is toward the development of extra setae and structures, whereas Libytheidae has lost several primary setae that were present in the Papilionoidea ancestor. The larvae of Nymphalinae have an enormous set of spines and antlers, and it seems impossible to derive Libytheidae larvae from them. Some first stage Satyrinae larvae (*Cercyonis*) have only one SD seta on thorax segments 2-3 as in Libytheidae, but these setae are vastly different in shape, and the older larvae and adults are much different. Deriving the Libytheidae from Danainae or other Nymphalidae seems equally difficult. Danainae lack horns and spines on larvae, but they have extra setae in the first stage larvae, and have fleshy filaments, plus specialized adult mating behavior, that make it extremely doubtful that the other Nymphalidae or Libytheidae were derived from them. Libytheidae have small patagia, whereas they are large in all Nymphalidae, membranous in Lycaenidae. The venation of Libytheidae is similar to that of Nymphalinae (Nymphalidae) and Styginae (Lycaenidae) so are of no help.

Evolution of Papilionidae

Papilionidae evolved from a common ancestor with the Pieridae (Fig. 3). After they split off of the Pierid line, the fw vein 2A ran to the hind margin instead of joining 1A. The second median plate (Fig. 2) was lost on the forewing base. On the head the labial sclerite usually became membranous in front of the palpi. The two cervical sclerites became joined beneath the neck. The spurs were lost on the tibia of the middle legs, and the pulvilli and arolium were lost on the legtips. The horizontal chamber of the adult aorta lost its enlargement and its two ostia (Hessel, 1969). The anepisternum was later often lost by various genera. On the metathorax the meral sulcus developed. Inside the thorax the topmost front-to-back wing muscle became larger than the others (pterothorax character #4 of Ehrlich and Ehrlich, 1963), and a muscle from the phragma of postnotum 2 to the abdomen base became tapered as it extends downward to the abdomen (pterothorax character #5 of Ehrlich and Ehrlich, 1963). The apophysis on abdomen segment 8 is not known in female Papilionidae (though its occurrence is spotty within other families). The larva developed the osmeterium to repel ants and other predators with the chemicals isobutyric acid and 2-methyl butyric acid (these chemicals present in *Baronia, Papilio, Eurytides,* Eisner et al., 1970; other chemicals are present also, Honda, 1983), and lost the ventral neck gland. The first-stage larva developed many extra setae on the side and above the prolegs, a trend that continued later and extended onto the head in some groups.

The Baroniinae (one Mexican species *Baronia brevicornis*) split off at this point, and developed some peculiarities, including many secondary body setae and many forked setae on the bumpy first-stage larval head (Ruiz, 1969; Vasquez and Perez, 1961), the antenna lost its scales, veins Sc and R_1 joined together on the forewing, one R vein disappeared, the tegumen and uncus became fused, the mesothoracic discrimen curved down in front of the furca slightly, and the prothorax furca arms lost the secondary anterior prong or lamella. *Baronia* retains a Pierid-shaped larva, a Parnassiinae-shaped pupa in an earthen cell, and feeds on the legume, *Acacia.* The Eocene fossils of *Praepapilio* were placed in a new subfamily by Durden and Rose (1978), but their poor state of preservation makes this doubtful (the

presence of CuP is especially dubious and the fore- and hindwings overlap confusingly in the fossils); they are best placed in Baroniinae, or perhaps in some other butterfly or Macrolepidoptera family.

In the remaining Papilionid line, vein 3A was lost on the hindwing (probably because of a scent fold which developed in that position, possessed now by *Eurytides* and *Parides* etc., which was later lost in Parnassiinae and scattered Papilioninae). In the prothorax, the spinasternum widened at the spina, the furcal arms developed a secondary anterior lamella or prong, and the intercoxal lamella migrated back to the furca, if the Papilionid ancestor lacked these three traits. Older larvae had red spots, tubercles, and ate *Aristolochia* (modern groups with tubercles and usually red spots are Parnassiinae: all Zerynthiini, and *Archon* in Parnassiini; Papilioninae: all Troidini, and in Leptocircini the *Protesilaus lysithous* group, perhaps *Graphium* which have spines on the thorax and rear, and some Papilionini which have small tubercles). Adults probably had a tail on vein M_3 and a female sphragis.

The Parnassiinae branched off here, and developed some unusual traits: mature larvae developed a carpet of setae and their osmeteria became non-functional (at least in *Parnassius*), the tarsal claws became asymmetrical, and females possessed a sphragis (five of eight genera now have it, as do some Papilioninae tribe Troidini). In at least *Parnassius*, two hooks developed on the forewing base (on the base of R and on the radial plate) to aid emergence of the adult from the silked or underground pupation site (the other genera should be examined for this trait). Two tribes, Zerynthiini and Parnassiini, are well founded (Ehrlich, 1958b; Hancock, 1983), though some traits Hancock cites are weak or have exceptions (patagia). Zerynthiini lost the scales on their antennae and legs; Parnassiini lost the tails, the larva pupates in debris or soil with a weak "cocoon", and the humeral vein became simple, the palpi a bit shorter.

The remaining line (Fig. 3), which became the Papilioninae, grew very large in size, adults continue to flutter while feeding at flowers (apparently an adaptation to their weight), the CuP vein ("cross-vein" or "basal spur") developed on the forewing base, probably to strengthen the larger wing (it is present in all butterfly pupae (Zeuner, 1943) but is rare in adults; in other butterflies a trace is present in Zerynthiini (Hancock, 1983), *Heliconius* (Emsley, 1963), etc.), and vein M_2 moved closer to M_3 than it was (M_2 was fairly close to M_3 in the Pap.-Pier. ancestor). The prothorax discrimen developed an anterior spine (if it was absent in the Papilionid ancestor). The pupa developed two blunt bumps on the head, and a dorsal thorax protuberance. Larvae retained fleshy filaments from the Parnassiinae ancestor. During the evolution of the Papilioninae, the first stage larvae acquired more and more extra setae, some of them on fleshy bumps (scoli).

The tribes within Papilioninae are still not very well founded despite the work of Ehrlich (1958b), Munroe (1961), and Hancock (1983). The controversy involves where Papilionini (P) arose, from the Leptocircini (L; = "Graphiini") stem or the Troidini (T) stem. The following traits support the origin of Papilionini from the Troidini stem, where Hancock places it: antenna unscaled in P and T, scaled in L; legs unscaled PT, scaled L; superuncus ("pseudouncus") always replacing uncus PT, seldom replacing L; patagia membranous or nearly so PT, largely sclerotized in most genera of L. The following traits support the origin of Papilionini from the Leptocircini stem: many secondary setae on first instar larvae (especially on the

head of *Papilio; Eurytides* and *Battus* have few secondary setae on the head;
Troidini has fewer on the body than the others) in LP, fewer in T, perhaps a weak
trait; mature larvae have red spots and tubercles in T, often lack them in LP, a
weak trait; hostplants usually Aristolochiaceae in T, never Aristolochiaceae in LP,
a weak trait. The tentorial crests are progressively higher in P, T, and L, the only
trait favoring the split of Papilionini before Leptocircini and Troidini split. Thus
Hancock's scheme has the most support, and another trait, the spine on the prodis-
crimen present in Papilionini and Troidini (except *Battus*) fits this scheme imper-
fectly. However, most traits supporting the scheme represent losses of structures,
so doubt remains. Other traits, including pigments, pupal shape, discocellular
vein position, humeral vein, precostal cell, metathoracic discrimen, signum, anal
fold scent glands, and tibia-tarsi spining, are too variable or the differences too
weak for them to be useful in tribal classification. (The character used to separate
Papilionini and Troidini in most keys, tibial and tarsal spining, seems useless,
because different legs, or inner and outer faces of the same leg, have as much varia-
tion in spining as the variation between tribes, and some *Battus philenor* legs I
examined have a spineless impressed lateral space, contrary to Munroe's and Han-
cock's keys.) Setal patterns on first-stage larvae should be studied much more. The
Troidini (*Battus* at least) switched osmeteria chemicals (they have beta-selinene
and selin-11-en-4alpha-ol, instead of isobutyric acid and 2-methyl butyric acid
possessed by Baroniinae and Papilionini, Eisner et al., 1970; Burger et al.,
1978).

Hancock's paper (1983) is a worthwhile contribution on Papilionidae, following
cladistic principles based on largely the same characters used by Ehrlich and Mun-
roe. However, Hancock's invocation of a special set of weak characters to create six
genera out of the single genus *Papilio*, characters different from those used to dis-
tinguish other genera of Papilioninae, surely is an act of "special creation". In
order to make the genera of Papilionini comparable to those of other tribes these six
genera should be returned to subgenera of *Papilio*. Minor points concerning Hancock
(1983) are these: *Praepapilio* is from the Green River Shale, not from Florissant, the
meral sulcus is characteristic of all Papilionidae, and Parnassiinae lack a prodis-
crimen spine. The antenna of Parnassiinae is 11.5 mm or shorter, the antenna of
Papilioninae is 11.0 mm or longer. Some of Hancock's "derived" traits may well be
primitive (the red-tuberculate larva, long palpi). Hancock states that the
"precoxal suture" (my secondary sternopleural sulcus) was present in the
Papilionid prototype, based on Ehrlich's (1958b) mention of it in Parnassiinae; but
it is not on the Parnassiinae I have examined and doubtfully occurs in any
Papilionid.

Evolution of Pieridae

Pieridae evolved from the line that also produced Papilionidae (Fig. 3). After the
Papilionidae branched off, the wings of the Pieridae ancestor probably were
colored with pterin pigments (the whitish, yellowish, and orange pigments present
in most species, and in other butterflies as well). The antenna muscles developed a
forward slant (character #10 of Ehrlich and Ehrlich, 1962). The antenna later
became pendulum-shaped in some groups. On the head the labial sclerite often
became membranous behind the palpi. Several R veins on the forewing branched
from each other. The claws on the leg tips forked in two (which happened in some

other families also, namely *Lamproptera curius* and *Meandrusa* in the Papilioninae, Acraeinae, and Aphnaeini in the Lycaeninae). The pulvilli (that were forked) joined into one wide pulvillus. The epiphysis on the foreleg was lost. On the prothorax, the two lateral plates of the pronotum became fused together only at the top (Ehrlich, 1958b), a muscle from the furca to the cervical sclerites was lost (prothorax character #1 of Ehrlich and Ehrlich, 1963), a muscle from the spinasternum to the coxa was lost (prothorax character #11 of Ehrlich and Ehrlich, 1963), and the spinasternum became widened into an oval in front of the spina. In the mesothorax the anepisternum was lost and a muscle to the postcoxal sclerite became attached to the scutum farther back (pterothorax character #6 of Ehrlich and Ehrlich, 1963). On the abdomen the prespiracular bar was lost, and sternum 2 moved forward more than in other families (though almost as far forward in Hesperiidae). The papilla analis apophysis retractor muscle shifted from segment 7 to 8 (Stekol'nikov, 1967). The pupa developed a single cone on the head, and the pupal wings probably expanded somewhat (see Aiello, 1980 for Dismorphiinae). The first-stage larva lost the second SD seta on the metathorax. Setae D1 and D2 of young larvae are forked and dispense honeydew (Forbes, 1916) to bribe ants (in Dismorphiinae, Coliadinae, and Pierinae at least, Ford, 1945).

The ancestor of Dismorphiinae and Pseudopontiinae branched off the Pieridae line at this point (Fig. 3). The patagia on the prothorax became membranous, and the peculiar male mating structures unique to both groups developed (tegumen short, uncus in two lobes, valvae fused ventrally). This ancestor was probably in both Africa and South America when they were joined; then, after the continents split apart, the African population ancestral to Pseudopontiinae developed rounded wings and a peculiar pattern of fusion of some wing veins (and lost two R veins), developed a linear (unclubbed) antenna, and the metathorax discrimen grew straight back to the furca (as in the mesothorax), while the American population ancestral to Dismorphiinae (of which one genus probably later spread to Eurasia across the Bering Strait) kept all five forewing R veins, but they joined up to one stalk (Dismorphiinae have other peculiarities also, including a very wide juxta, and only one SD seta on both mesothorax and metathorax, the major setae T-shaped). Dismorphiinae retained the forewing vein M_2 closer to M_3 of the Papilionid-Pierid ancestor (see Klots, 1931), while in the other Pierid subfamilies M_2 moved toward M_1. Pseudopontiinae contains just one species, *Pseudopontia paradoxa*, a rounded-wing white West African forest species.

After those subfamilies branched, the ancestor of Pierinae and Coliadinae developed a tiny bump on the forewing base (which Sharplin, 1963a calls a remnant of the M vein) that separates the base of the Cu vein from the radial plate, a trait unique to Pierinae and Coliadinae among the butterflies and skippers (Sharplin, 1964 claimed that all Papilionoidea have it, but she examined only *Pieris*; I examined the other subfamilies and families for this trait). First-stage larvae lost the second prothorax L seta. Females developed unique lobelike scent glands on the female abdomen tip to repel males (females spread the wings and raise the abdomen to waft the scent). This line then split into Pierinae and Coliadinae. The Pierinae developed a more clubbed antenna (usually) and a longer tegumen, the patagia became membranous, and the uncus hinges on the tegumen, flexing down and forward (in *Pieris* and *Anthocharis*, Stekol'nikov, 1967; *Neophasia*, this paper). The Coliadinae nearly lost the humeral vein, the last palp segment shrank, a "raised line" developed (Klots, 1931), and the juxta expanded at the tip.

Anthocharis and *Euchloe* have sometimes been placed in a different tribe ("Euchloini", Klots, 1931) or even subfamily, but their similarity in morphology (Ehrlich, 1958b), appearance, habits, and Cruciferae hostplants to *Pieris* places them in the Pierinae. Geiger (1981) studied 20 different body enzymes of 23 species of Pierinae, Coliadinae, and Dismorphiinae, and found that the differences between *Anthocharis* and other Pierinae are equivalent to the differences between other genera of Pierinae. Stekol'nikov (1967) thought that the similarity of "Euchloini" and Pierini in genital musculature indicated very close relationship.

Evolution of Nymphalidae

Nymphalidae evolved from the ancestral line that produced Lycaenidae and then Libytheidae (Fig. 3). After Libytheidae branched off, the female forelegs of the Nymphalid ancestor became small (the male forelegs became small earlier). The prothorax kept the sclerotized patagia of the butterfly ancestor, and the mesothorax anepisternum was present. The first stage larva kept the setae of the ancestor of all butterflies and skippers, except a few Satyrinae (*Cercyonis*), later lost one of the two SD setae on thorax segments 2-3, and first stage larvae later developed horns or tails or fleshy bumps or extra setae in some groups.

The first group to split from the Nymphalidae line was the ancestor of Danainae and Ithomiinae. (Waterhouse, 1953 also thought that Danainae branched off prior to Satyrinae and Nymphalidae because of its primitive type of adult peritrophic membrane.) Danainae-Ithomiinae obviously form a monophyletic group, and should best be lumped into one subfamily. Their ancestor developed fleshy filaments on the larva, except that *Anetia* of the Danainae and *Hymenitis* etc. of the Ithomiinae lack them today. Some species of both subfamilies now have only mesothorax filaments and have nearly identical larval color patterns (Young, 1981). Their ancestor developed a few secondary setae on the first stage larva, at least in *Danaus* (extra D setae) and (Müller, 1886) *Ithomia*. The males developed the unique habit of seeking a chemical (lycopsamine) from plants in order to make their male pheromones, which are distributed by hair pencils on the abdomen or wings (Edgar, 1975). Edgar thinks that the hostplant of their common ancestor (probably Apocynaceae, which some genera of both subfamilies eat today) had both lycopsamine for mating and cardenolides for poisoning predators (adults are models in mimicry), then the plants stopped producing lycopsamine to lessen larval feeding damage by forcing the adults to search for it elsewhere (adults must now obtain it from other plants such as heliotrope). Then most Ithomiinae switched to Solanaceae and most Danainae to Asclepiadaceae.

The mesothoracic anepisternum was lost in the Danainae-Ithomiinae ancestor, the meron developed a bulge above a caudal constriction, and the hypopteron became small. The anterior arms of the tentorium became small. This line then split into the ancestors of Danainae and Ithomiinae, and they then developed some peculiar traits, such as the scaleless antenna and abdomen hair pencils of Danainae, the fine dorsal tarsal spines (Forbes, 1939) and (often) dorsal hindwing hair pencils of Ithomiinae. Gilbert and Ehrlich (1970) note that adults of both subfamilies tend to feign death when handled (not a unique trait; I observed it frequently in *Poladryas minuta* and *Polygonia*, Nymphalinae, and it is recorded in *Nymphalis antiopa* and others).

Returning to the Nymphalid line, the larva developed two tails and two head horns, which most of the remaining Nymphalidae have (Ashizawa and Muroya, 1967 illustrate the tails and horns of Calinaginae). The adult peritrophic membrane now delaminated from the midgut epithelium (Waterhouse, 1953, though undetermined in Calinaginae). The anterior part of the adult midgut developed many processes (noted in Satyrinae, Apaturinae, and Nymphalinae by Homma, 1954; apparently absent in Danainae, Ehrlich and Davidson, 1961). Apparently the Calinaginae branched off next. Calinaginae seem to closely resemble what the ancestor of the remaining Nymphalids was like, although some derived characters are present (the gnathos is absent, and an extra uncus occurs above the usual uncus). The remaining Nymphalidae line then completely lost the claws on the female prothoracic legs (a weak trait, as claws occur in very few Nymphalids that split off earlier, namely Calinaginae and a few Ithomiinae which have small claws).

The ancestor of Satyrinae and Morphinae branched off next. The larvae of this ancestor began feeding on monocotyledons (although some, but not all, *Morpho* species later switched back to dicotyledons), and the adults probably developed many eyespots (which occur in most Satyrinae and Morphinae today), and developed a simplified toothed male valva. The line then forked, and the Satyrinae developed their swollen forewing veins, reduced hypopteron and anepisternum, and enlarged third larval eye, while the first stage Morphinae larvae grew a "fuzzy" head with hundreds of setae (forked at least in *Morpho,* Müller, 1886, and larvae raised and loaned by Allen Young) and added a few extra setae on the body (at least the hair-tufts present in *Morpho*).

The Brassolini have been placed in Satyrinae by Miller (1968), in Morphinae by Ehrlich (1958b). Some traits listed by Ehrlich support placing Brassolini into Morphinae (the hypopteron is well-developed, the mesothoracic anepisternum is larger, and the forewing veins are not swollen at the base). *Opsiphanes* (Brassolini) first-stage larvae have a fuzzy head (with hundreds of setae) (Casagrande, 1979; and photos by Allen Young) as do *Morpho* (Müller, 1886 illustrates single *Morpho* head setae, some multiply-split to the basal socket). The fuzzy head is so unusual (apparently unique) that I suggest it defines Morphinae (including Brassolini) as a monophyletic group. Morphinae also have a general propensity for communal larval feeding. Satyrinae clean the antenna by stepping on it while the antenna is pulled beneath the leg (Jander, 1966), which other subfamilies such as Morphinae may also do. Vane-Wright (1972) notes similarities of male abdominal hair pencils and egg shape between certain Biini ("Satyrinae") and Morphinae, so Biini may belong to Morphinae as well, though other characters should be examined also (abdominal hair pencils are also present in Danainae and such Nymphalinae as *Biblis*).

After the Satyrinae-Morphinae branch split off, the remaining line lost the veins closing the end of the discal cells. This character seems rather easily changed, as most Morphinae and some Satyrinae, both of which branched off prior to this point, have an open hindwing cell, and some descendants from the present ancestor regained a closed hindwing cell, namely Acraeinae and *Heliconius,* or a closed forewing cell, namely some Nymphalinae and Acraeinae. The male saccus may have lengthened (it is longer than the valva in European Charaxinae and Apaturinae). Young larvae developed the peculiar habit of silking dung pellets to a

leaf vein (known in Charaxinae, Apaturinae, Nymphalinae; Acraeinae probably have this habit, observations are needed). Then the Charaxinae branched off, and reacquired sclerotized parapatagia on the prothorax (one Nymphalinae genus also acquired them). The plump flanged pupa developed. Some first-stage Charaxinae larvae have secondary setae, horns and tails, but others lack these features. Some Charaxinae (*Hypna*, Young, 1982) have fleshy tubercles on older larvae, with a single spine on each tubercle of mature larvae, apparently independently evolved from the scoli of Nym.-Acra. (Acraeinae) which have many spines on each scolus.

The remaining Nymphalidae line then changed somewhat. The antenna may have become pendulum-shaped (except the clubs are more rodlike in *Limenitis, Doxocopa*, and others now), the anterior tentorium arms in the head started a thinning trend, and the mesothorax anepisternum disappeared.

Apaturinae split off at this point, and their larvae kept the two tails and two head horns of most Charaxinae, Morphinae, most Satyrinae, and Calinaginae, which branched off previously. Apaturinae have been treated as a tribe of Nymphalinae, as a subfamily of Nymphalidae, and even as a separate family. The adult traits are like those of Nymphalinae (Ehrlich, 1958b); however the larvae lack the branching spines of Nymphalinae. Other workers combine Apaturinae with the Charaxinae (which is untenable cladistically, violating the second principle of cladistics listed above, because Nymphalinae-Acraeinae is the sister-group of Apaturinae), but Ehrlich (1958b) found that the parapatagia on the adult prothorax are membranous, and there is no distinct anepisternum on the adult mesothorax, which distinguishes adults from adults of Charaxinae. The pupae differ greatly (Mosher, 1916), being flattened sideways except in the smaller species. The ancestral Apaturinae larva possibly ate *Celtis*. The larval and pupal traits warrant treating Apaturinae as a separate subfamily, related to Nymphalinae and to Charaxinae, and cladistic principle #2 requires this teatment. The main problem concerning Apaturinae is whether they are merely a minor branch (perhaps a tribe) of Nymphalinae which has lost the larval body spines of Nymphalinae. Of course all the genera with a spineless body could be placed in Apaturinae and the spined genera in Nymphalinae, but the correctness of such pigeonholing must depend on whether other characters produce the same subfamily assignments. The elongated cremaster of most *Asterocampa* is limited to a few genera of Apaturinae so does not help, but all Apaturinae have a particular arrangement of branches on the antlers of the larval head (T. Friedlander pers. comm.). Some Apaturinae genera (*Hestina, Sasakia,* etc.) have apparent paired "scoli" on the larval body, but T. Friedlander (pers. comm.) states that these are merely fused bases of chalazae, a chalaza being an integumental hill beneath a seta, and thus are probably not homologous with the true scoli of Nym.-Acra. and seem to represent incipient scoli.

The remaining line, after Apaturinae split off, then evolved branching spines (scoli) on the larval body (the head scoli perhaps required little modification from the horns of the Apaturinae ancestor), and the two larval tails were lost. The function of these tails has not been explained, but if we assume that they were used for camouflage, perhaps eliminating the shadow at the rear, or simulating leaf veins, they became useless as the larva's strategy shifted to conspicuous spines for armored defense. The male saccus apparently shortened. The ancestor then split

into two lines, Acraeinae and Nymphalinae, at this point. Both lines have a tendency to lose their arolium and pulvilli. Acraeinae have branching spines on the larval body (and often on the pupa), and other traits resemble those of Nymphalinae, except that they developed some peculiarities such as forked or asymmetrical leg claws. The pulvilli and arolium usually disappeared, the mesothorax anepisternum was lost, the anterior tentorial arms became thinner, the gnathos nearly disappeared, the abdomen elongated and the hindwing lost its abdominal flap, the female often developed a sphragis, and the discal cells on the wings became closed by cross veins.

Acraeinae is closely related to Nymphalinae cladistically (the larval scoli define Nym.-Acra. as a monophyletic group), and most genera of both subfamilies have only primary setae in first-stage larvae, but phenetically Acraeinae differs by an accumulation of these odd (mostly lost) traits. Acraeinae may actually not be a distinct subfamily; but just a side branch within Nymphalinae, perhaps near Heliconiini. Ehrlich (1958b) notes that Heliconiini falls in a continuum between Acraeinae and Argynnini, with the largest gap between Acraeinae and Heliconiini.

The remaining line is the Nymphalinae. I can draw no conclusions regarding the tribal evolution within this subfamily, except for the close relationship of Heliconiini and Argynnini. Such groups as Biblidini, Eurytelini, Limenitidini, Marpesiini, etc. (these names are properly spelled, J. Eliot pers. comm.) may not even be valid phenetically. The larva of *Marpesia petreus* is unusual, but that of *M. chiron* is like other Nymphalinae. *Limenitis arthemis* and relatives (and *L. ("Adelpha") isis* and *plesaure,* Müller, 1886) differ grossly in larva and pupa traits, but *L. ("Adelpha") bredowii* connects them to other Nymphalinae. A good generic classification is needed, including some new characters, such as the structures and habits of larvae and pupae.

The tribe Heliconiini of the Nymphalinae has often been elevated to family status, but probably evolved from a species similar to living *Euptoieta* but silverspotted, the same species also producing the tribe Argynnini. This progenitor had androconial scales on the dorsal veins of fore- and hindwings of males, and the female had a dorsal scent gland between abdomen segments 7 and 8 used for mating. The male had a well-developed uncus (Emsley, 1963; dos Passos and Grey, 1945; the uncus is absent in Melitaeini at least in the European and American groups I am familiar with). Larvae lacked middorsal branching spines, and undoubtedly ate Passifloraceae and Turneraceae, which both tribes (*Euptoieta* among the Argynnini) eat today. In America there are two lines descended from this progenitor. The first line, Heliconiini, has humeral vein aimed toward the body, and, after *Dryadula* branched off, it evolved the female stink club on sternum 7 to repel males. This club swings up into the dorsal scent gland when not in use, and during mating fits into male valval glands (Emsley, 1963), where it picks up some chemical to activate the "stink" of mated females. The second line leading to Argynnini lost the branching spines on the larval head, and after *Euptoieta* branched off, females began to oviposit haphazardly near their hostplants, while first-stage larvae became the overwintering stage and developed extra (secondary) body setae. One can see the evolutionary progression in number of setae within Argynnini even today: *Boloria titania* has few secondary body setae, *B. eunomia* and *freija* have more, and *B. improba* and *Speyeria* have still more. Some species

of both tribes lost the silver spots. These two tribes are so similar that the wing veins of *Dione* (Heliconiini) and *Euptoieta* (Argynnini) are identical (except for the humeral vein): the five R veins branch from one stalk, a feature found in no other butterflies except the *Phyciodes frisia* group. Further, dos Passos and Grey (1945) note that *Euptoieta* is somewhat intermediate between the tribes in male genital structure. However, the picture in Asia differs (J. Eliot, pers. comm.). *Vindula* and *Cirrochroa* have the humeral vein forked (one branch proximal, the other distal), probably the condition in the progenitor of Heliconiini/Argynnini. *Vindula, Cethosia,* and *Terinos* have very long branching spines on the larval head, but the last two have a distally-directed humeral vein, although *Cethosia* (and *Vindula*) feed on Passifloraceae. Other Oriental "Argynnini" have branching head spines also. Evidently the tribes Heliconiini and Argynnini cannot be sustained on a worldwide basis, and the hostplant, humeral vein, and head spines are not consistent. Therefore, the two tribes probably should be combined into one, Heliconiini (by priority). Whether this combination is a monophyletic group remains to be determined. No doubt those Heliconiini with a stink club do represent a monophyletic group (perhaps including *Dryadula* which later lost it?). Certainly, elevating Heliconiini to family level is absolutely ludicrous.

Evolution of Libytheidae

Libytheidae evolved from ancestors which later produced Nymphalidae (Fig. 3), and the two families share many traits, such as antenna ridges. After the Nymphalidae ancestor branched, the first-stage larva developed a wide flange behind the head, and the second SD seta was lost on thorax segments 2-3. The palpi grew longer. On the prothorax, a muscle from the furca to the head rim became fan-shaped (prothorax character #9 of Ehrlich and Ehrlich, 1963), and the patagia became partly membranous. On the mesothorax, the preepimeron (Fig. 1) of Nymphalidae and Lycaenidae was modified (the function of the sulcus was taken over by thickening of the exoskeleton there; Ehrlich, 1958b draws a line illustrating this), the anepisternum was lost, and the postmedian wing lever (Fig. 1) became arrowhead-shaped. The mesothorax greatly overhangs the metathorax, which may provide more flight efficiency for migrations. A superuncus evolved on male abdomen segment 8. The mature larval prolegs have some crochets on the lateral side.

Evolution of Lycaenidae

Lycaenidae evolved from the butterfly line that also produced Nymphalidae and Libytheidae (Fig. 3). The Lycaenid ancestor was evidently small in size. The eyes stayed large for good vision while the head shrank, thus the eyes became notched (or at least the eye touches the antenna socket) after Styginae split off to allow room for the antennae, the frontogenal sulcus crowded against the eye, and the face became less arched. The labrum became small. The small size of the legs led to the pulvillae becoming single instead of forked.

The forelegs were obviously small in the lycaenid ancestor, because Jander (1966; see Fig. 15) found that Lycaenidae clean their eyes and antennae with the middle legs, even in living species (Polyommatini) with large forelegs, thereby suggesting that the forelegs were too small for cleaning when this behavior evolved. Special scale-brushes are on the middle leg for cleaning the antennae, a tuft of scales on the

femur opposed to an oblique trough-like scale brush on the tibia as noted by Eliot (1973) in nearly all Lycaeninae, and present in the same form in Riodininae in *Thisbe, Baeotis, Theope*, etc., and with the tibial brush reduced in many others. The femur brush at least was present in the ancestral species that gave rise to Lycaenidae, Nymphalidae, and Libytheidae, because all three clean the antenna with the middle legs, and the femur tuft is strong in Libytheidae and reduced or absent in Nymphalidae. The tibial brushes are absent or very weak in Nym.-Lib., though noticed by Ehrlich (1958a) in Danainae, so seem to have been well-developed only by Lycaenidae. Curetinae pupae have the middle leg touching the eye as in Nymphalidae (Shirozu and Yamamoto, 1957), which also suggests a small foreleg in the Lycaenid ancestor. The segmentation of the male foreleg of the Lycaenid ancestor is controversial, because today only the Styginae, a few Riodininae, some Miletini, all Liphyrini, very few Theclini, and Polyommatini have a segmented and clawed male foreleg tarsus (the "claw" just a single prong in Polyommatini), and the rest (including all Curetinae, Liptenini, Poritiini, Aphnaeini, and Lycaenini) have the tarsus reduced to one unclawed segment. It is traditional to assume that the segments and claws were independently lost many times. However, at least some Theclini seem to have reacquired segmented and clawed male forelegs (Eliot, 1973, pp. 394-395, perhaps by acquiring them using either mesothorax or female genes, females having fully formed forelegs. If genes for the segmented leg were on the Y chromosome, males could acquire the genes from crossing-over to an X chromosome (Eliot, 1973; as in Lepidoptera females are XY, males XX). The view that the Lycaenidae ancestor had only one unclawed tarsal segment on the male foreleg, and later lycaenids sometimes reacquired them, accords with the degenerate male foreleg of Libytheidae and Nymphalidae.

On the prothorax the patagia became membranous, and a muscle from the apodeme of the pronotum attached to the prescutum of the mesothorax much more to the side (prothorax character #7 of Ehrlich and Ehrlich, 1963). In the mesothorax the discrimen curved down to the base of the furca (apparently by using genes from the metathorax), and a muscle from the scutellum to the postnotum straightened (it was twisted; pterothorax character #7 of Ehrlich and Ehrlich, 1963). The male testis became white or yellow instead of red (Ehrlich, 1961). An elongate uncus is retained in Styginae, Riodininae, Curetinae, some Theclini and Polyommatini (J. Eliot pers. comm.), but the male uncus later became bilobed in many groups. A transtilla developed over the male valvae.

The pupa retained the silk girdle of the ancestor of butterflies and skippers (though it was later lost in many groups), and the pupal head has a tendency to become more ventral. Older larvae had a carpet of short setae, though the Liptenini-Poritiini and some Miletini and American Riodininae later developed long setae. The larval prolegs developed a unique fleshy lobe to help these small larvae stick to smooth surfaces such as fruits. The ventral neck gland was lost on the larva. The Lycaenidae ancestor probably ate plants, because carnivorous habits occur only in a few tribes of Lycaeninae, whereas plant-feeding is widespread. The lycaenid ancestor probably did not eat aphids (or other honeydew-producing bugs that are also tended by ants for honeydew), because this behavior is uncommon, and lycaenids that eat them today (Miletini) lack the honey glands and tentacles (Clark and Dickson, 1956) that were undoubtedly present in the lycaenid ancestor. The larvae became associated with ants, probably because the ancestor fed on flower buds and fruits and had to deal with ants that came to feed

Families   **Subfamilies**   **Tribes**

Papilioninae — Leptocircini
Papilionini
Troidini
Parnassiinae
Baroniinae
Pseudopontiinae
Dismorphiinae
Coliadinae
Pierinae
Danainae
Ithomiinae
Satyrinae
Morphinae
Charaxinae
Apaturinae
Nymphalinae
Acraeinae
Calinaginae
Libytheidae
Styginae
Riodininae
Curetinae
Lycaeninae
Liptenini
Poritiini
Miletini
Liphyrini
Aphnaeini
Theclini
Lycaenini
Polyommatini
Megathyminae
Hesperiinae
Pyrginae
Coeliadinae
Pyrrhopyginae

Papilionidae *Pieridae* *Nymphalidae* *Libytheidae* *Lycaenidae* *Hesperiidae*

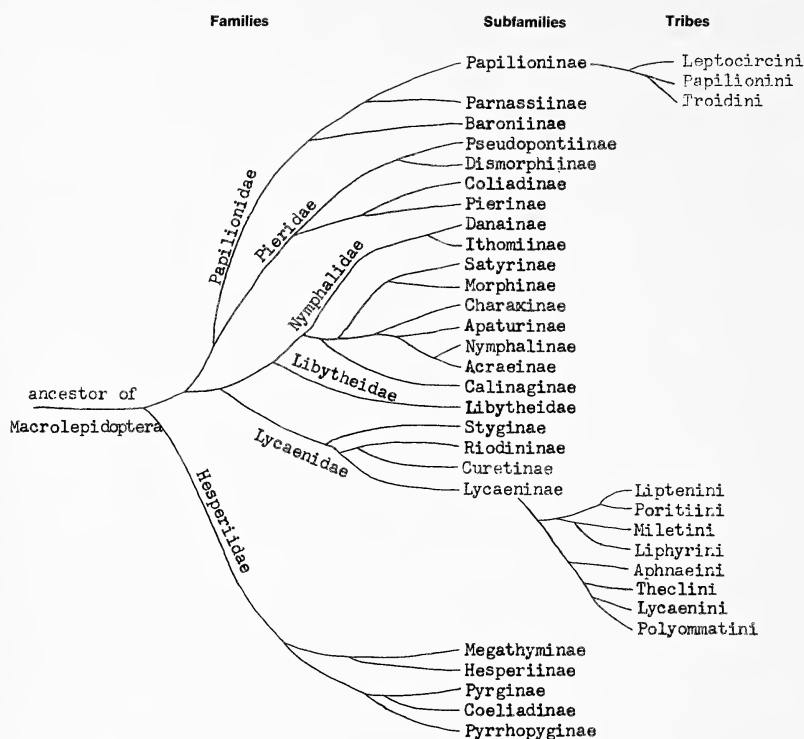ancestor of
Macrolepidoptera

Fig. 3. Phylogeny accepted. The branching sequence represents inferred
genealogy, whereas the sequence from top to bottom represents (as
much as possible given the genealogy) the "distance" phenetic tree of
Ehrlich, 1967.

on flower nectar (flower-fruit feeding would explain the small size of lycaenid
adults also, because most plant fruits are small). At any rate, the association with
ants caused the development of very thick skin to prevent damage from ant bites
(Liphyrini and some Miletini later developed an even stronger armored skin),
"performed cupolas" (microscopic glands that cause ants to touch the larva), honey
glands (Newcomer's gland and "dew patches", that produce honey to bribe the
ants), and eversible tentacles that apparently produce chemicals mimicking ant
alarm pheromones to cause the ants to disperse (Malicky, 1970). These glands are
present in both Riodininae and Lycaeninae. Riodininae have other glands called
"vibratory papillae" on the prothorax (Ross, 1964). Curetinae possess eversible
tentacles on very long pillars on abdomen segment 8, a tear-shaped supra-
spiracular pit on each side of segment 8 that may be a honey-gland, and an odd
translucent platelike organ (hollow beneath) above each spiracle on abdomen seg-
ment 7 (*Curetis acuta*, J. Scott, unpubl.). The association with ants also started a
trend in larval shape, in which the head retracted into the thorax (except in
Liptenini-Poritiini), probably to avoid ant attack (and the upper setae of the head
shrank in order to fit the head into the prothorax). Ants began to tend lycaenid lar-

vae like cows, sometimes moving them about and even moving them into the ant nest. This allowed some lycaenid larvae to use ant larvae for food. The sudden drop of ripening fruits encouraged cannibalism (fallen larvae died, and the ones remaining on the plant had to cope with little food), which is frequent when lycaenid larvae are crowded. Fruit-feeders often cope with this by timing egg-laying on the flower buds so that most larvae mature before fruit-drop; in some cases the larva silks the fruit securely to the twig (J. Eliot, pers. comm.). Carnivorous habits led some Lycaenidae (Miletini, rarely others) to eat Aphididae and other plant-sap-sucking Homoptera as their only larval food. The hypostomal bridge on the larval head developed a unique wide gap. The first instar larva head generally nearly lost the F1 seta [lost in most Lycaenidae, present but extremely small in *Lycaena* first instars (Wright, 1983), and present in older larvae] which all other families have. The body developed chitin rings [=annuli=lenticles, apparently glandular structures (Wright, 1983), which may be related to perforated cupolas] and many extra setae including SV setae above the prolegs, and abdomen segments 9-10 generally became somewhat fused in appearance.

The first group to evolve from the lycaenid ancestor, most likely on the American side of Pangaea, was apparently the Styginae, which today is represented only by one large rounded-winged gray Andean species, *Styx infernalis*. Styginae retain various primitive characters, such as a large anepisternum, five radial veins, a wide face so that the eyes are not notched, a segmented and clawed male foretarsus (but the male foreleg is small, less than half the size of the middle leg), a humeral vein, tibial spurs, and a transtilla (the genitalia resemble those of Riodininae and Curetinae, J. Eliot, pers. comm.). In addition, Styginae are larger than most lycaenids, and there is a possibility that the larvae lack the ant adaptations such as thick skin and the various ant glands which may have evolved later. The Styginae also developed specialized traits, such as an ungrooved antenna, short palpi, the labial sclerite membranous in front of the palpi, short blunt tegulae, and two recurrent M veins in the forewing cell. One character, the very small male foreleg, suggests that Styginae arose from the base of the Riodininae line, and another, the ungrooved antenna, suggests that it arose from the base of the Lycaeninae line, but it seems best placed prior to both, certainly until its early stages are known.

After Styginae branched off, the lycaenid line then developed a slightly smaller anepisternum, characteristic of Riodininae and Curetinae, and the eyes became generally notched beside the antennae. The larva developed the ant-adaptations, if they were not developed earlier. The next to branch off was the Riodininae line. Eliot (1973) suggests that the ancestor of Riodininae and Lycaeninae existed before South America finally split from Africa in the Cretaceous, and then the Riodininae evolved mainly in America (only about 50 species are in the Old World), while the Lycaeninae evolved in the Old World. However, because Curetinae is Oriental, all three must have evolved before the split, and then each of the three survived only on one side of the split due to extinctions. Most American Lycaeninae belong to one group of Theclini which developed from perhaps only one ancestor that came into South America from Africa across the growing Atlantic Ocean (Eliot, 1973). Apparently *Brephidium, Leptotes,* and *Hemiargus* may have migrated or been blown from Africa to America in the late Tertiary, as they have not developed many American descendants, Eliot, 1973; *Feniseca* and *Zizula* also have few descendants and are related to African groups, or they may simply be old taxa that speciated little or most species died out. Some American lycaenids are

descended from ancestors that came across the Bering Strait from Asia (two Theclini, *Hypaurotis* and *Habrodais*, the Lycaenini, and most of the Polyommatini), and some American groups went the other way to Asia.

The Riodininae line evolved their characteristic spinelike projection of the male prothorax coxa below the trochanter. (The Curetinae probably branched off after this development, see below.) The male foreleg of Riodininae then became brushlike (with long scales), less than half the length of the middle legs, and the tarsus became reduced (rarely clawed, four-segmented to unsegmented today). The hindwing developed a short costal vein in addition to the humeral vein. Late instar larvae developed extra setae on the mandible (a dozen in *Apodemia*; some first-stage larvae such as *Apodemia,* and Curetinae and Lycaeninae and other butterfly and moth larvae have only two setae), "vibratory papillae" developed on the prothorax of some species (Ross, 1964) that pop out when ants are near. The typical positions of the ant-related glands changed in Riodininae or Lycaeninae, because they differ in the two groups. Newcomer's gland is on abdomen segment 8 in Riodininae and apparently in Curetinae, on segments 5-8 but usually on 7 in Lycaeninae. The eversible tentacles are on the metathorax and sometimes the rear in Riodininae, on abdomen segment 8 of Curetinae, on abdomen segment 7 in Lycaeninae. The Riodininae retained some primitive traits such as one groove on the antenna, an elongate uncus and a transtilla, plus tibial spurs.

In the Old World branch (Fig. 3) leading to Lycaeninae, the male foreleg stayed or grew a little larger (greater than ½ the length of the other legs), and the antenna lost its groove. The late instar larva retained the two mandible setae of the lycaenid ancestor. The Curetinae doubtfully branched off at this point, if so, the male foreleg of the Lycaeninae ancestor lost the coxal extension past the trochanter that the Lycaeninae line must have had to produce this state in Curetinae. In the Lycaeninae line, now the anepisternum became small or absent, and the usual positions of the ant glands changed as noted above.

So far, two points of origin of Curetinae have been proposed, from the base of the Riodininae line, or the base of the Lycaeninae line (I agree with Shirozu and Yamamoto, 1957, that Curetinae is a distinct subfamily, phenetically between those subfamilies). A number of traits of Curetinae support its placement at the base of the Riodininae line: the male foreleg coxa extends below the trochanter nearly as far as in Riodininae, the male foretarsus is reduced (fused to a single unclawed segment), Newcomer's gland is on abdomen segment 8 in larvae of *Curetis acuta*, the anepisternum is fairly large (as in Riodininae), and the male genitalia are very similar (Shirozu and Yamamoto, 1957) with an elongate uncus and a true transtilla. However, some traits support its placement at the base of the Lycaeninae line: the antenna is ungrooved (an independent loss as in Styginae?), the older larval mandible has only two setae as two is the primitive state, and the male foreleg is larger than in Riodininae (this is probably the primitive state) and shaped as in many Lycaeninae with a tapered down-curved point. However, according to the leg theory of Eliot, 1973 and adopted in this paper, the Curetinae, Riodininae, and Lycaeninae independently evolved the fused clawless male foretarsus, so any similarity in shape is due to convergence. Most of these traits are primitive and thus unusable cladistically. Nevertheless, the extended male foreleg coxa is a derived trait perhaps unique in Lepidoptera, and definitely favors the Riodininae position. If this position is correct, principle #2 requires that Curetinae

be raised to subfamily rank. At any rate, Curetinae retained tibial spurs, but lost the humeral vein, and the antenna developed ventral bristles on the basal 3-4 segments. The middle leg of the pupa touches the eye as in Nymphalidae and Libytheidae (Shirozu and Yamamoto, 1957). The larvae eat green plants rather than other insects. The first-stage larval setae are mostly arranged as in some Lycaeninae. With the current state of knowledge, the large variation in setal patterns in Lycaenidae, especially in Riodininae, has defied analysis.

Returning to the Lycaeninae line, the true transtilla was lost, and then the Liptenini-Poritiini-Miletini-Liphyrini branch split off (Fig. 3). However a few members of this branch possess structures that are perhaps rudiments of a transtilla, so the last gasp of the transtilla may have been in the Lycaeninae line after this branch and prior to Aphnaeini. In any event, this branch lost the tibial spurs, and lost the larval honey glands, but retained the humeral vein. The Mil.-Lip. (Miletini-Liphyrini) stem then split off of this branch. Mil.-Lip. larvae are carnivorous, but generally eat different animals, Homoptera and ants respectively (except that *Aslauga* of the Liphyrini eats coccids farmed by ants, and some Miletini have been found in ant nests). The Liphyrini might be placed on the main Lycaeninae line prior to Aphnaeini, but the larvae of some Miletini (*Miletus*) have a tough leathery carapace which J. Eliot (pers. comm.) states is about intermediate between the extremes represented by *Thestor* (Miletini) and *Liphyra*. The characters that favor Liphyrini being placed on the main Lycaeninae line (larval tentacles, length of larval setae, humeral vein, transtilla?) are very weak, because most Miletini and Liphyrini genera are identical in these traits (see Eliot, 1973). Miletini larvae began to prey on Homoptera (Aphididae, Coccidae, Membracidae, Cicadellidae), and the larvae and adults of some (*Lachnocnema, Allotinus, Miletus*) even stroke these Homoptera to obtain honeydew. A "transtilla" is present in *Feniseca* and perhaps other Miletini, though whether it is homologous to the Styginae-Riodininae-Curetinae true transtilla is questionable. *Feniseca, Spalgis,* and *Taraka* developed some long larval setae, but other genera are short-haired and shaped as in other Lycaeninae. Some genera retained a segmented clawed male foreleg. The Liphyrini branch always retained segmented clawed male forelegs, but lost the humeral vein, and there is no trace of a transtilla. Their larvae apparently have cupolas, and *Aslauga* has tentacles. Larvae live in ant nests and have a leathery flange on the sides that droops to the ground to protect them from ants (larvae eat ant grubs). The pupae are attached only by the cremaster (or are inside the larval skin).

The Lipt.-Por. (Liptenini-Poritiini) line evolved a larva with a large non-retractable head and tufts of long setae, perhaps for protection against wasps and predators needed because of the loss of ant protection, although the larva of *Teratoneura*, Liptenini, has urticating dorsal setae on abdomen segments 1-4. The pupa became attached only by the cremaster, the male foreleg tarsus shrank to one unclawed segment, the saccus became aimed to the rear, and a sheath developed above the aedeagus (doubtfully a transtilla) that attaches to the bottom of the valvae. The line then split into two tribes, the African Liptenini whose larvae eat lichens and microscopic fungi (*Teratoneura* adults sip Coccid honeydew), and the SE Asian Poritiini whose larvae gregariously eat dicotyledon plants (the Poritiini developed ventral tufts of bristles on the abdomen tip, and spinelets instead of spurs on the end of the tibia).

Returning to the main Lycaeninae line, the transtilla was definitely lost at this point (if not earlier), the humeral vein disappeared, the proboscis lost nearly all of its setae, the hindwing probably developed tails, "hindwing rubbing" may have evolved, "dew patches" (honeydew glands) apparently developed on the larva, and the male foretarsus became a single unclawed segment (segments and claws were later regained by Theclini and Polyommatini). Aphnaeini branched off here. Aphnaeini were placed in Theclini by Eliot (1973), but I place them as a sister-group of Theclini-Lycaenini-Polyommatini because they have a cylindrical larva with a rather large non-retractable head, the male genital muscles differ from the latter three tribes (A. Sibatani, see Eliot, 1973, p. 470), five radial veins are retained from the lycaenid ancestor (as in Liptenini, some Poritiini, and Liphyrini), and the larval tentacles pop out of mounds as in some Liphyrini. Eliot (1973, p. 470) notes that the endodont of the tarsal claw is more prominent than in Theclini. This placement of Aphnaeini will be confirmed if adults are found to lack "hindwing rubbing"; the exact taxonomic distribution of this cladistically valuable trait must be determined. The Aphnaeini developed a few peculiarities also (a semi-membranous band connecting the two valvae in most genera, the leg claws are bifid, the underside generally has metallic spots). The larvae eat green plants (rarely ants).

The remaining Lycaeninae line lost one radial vein, and certainly (if not prior to Aphnaeini) developed "hindwing rubbing" to draw predators' attention to eyespots and the antenna-like tail. At last the Theclini branched off, and some of these apparently regained a segmented clawed male foretarsus. Then the remaining line developed a flattened antenna club, and split into Lycaenini and Polyommatini.

There are insufficient good characters to be really confident of the tribal classification within Lycaeninae, as many characters represent losses of structures, and others are weak. The first stage larvae show such extreme variation that even they are not helpful at the present time. The presence or absence of a silk pupal girdle has not been used in this analysis because it seems a very weak trait (it is absent in all Liptenini, Poritiini, and Liphyrini, but present in some genera of all other tribes) because of its spotty occurrence in all groups.

Characters with Multiple Changes

An ideal cladistic classification is one in which each trait changes only once, and there are no reversals, parallel variation, or other complications. However, in most large taxa some characters do show parallel variation and reversals. It is worth examining these to make sure that the phylogenetic tree adopted is not incorrect.

The "lamella of the discrimen", a ridge in the bottom of the meso- and metathorax, is one such character. This discrimen curves downward to the base of the furca in the metathorax of all skippers and Papilionoidea, except *Pseudopontia* and to a slight extent in certain Papilioninae. The discrimen in the mesothorax curves downward to the furca in moths, skippers, and Lycaenidae (it curves down slightly in *Baronia* of the Papilionidae), but in the other Papilionoidea it runs straight back to the furca (Ehrlich, 1958b). The primitive state is for the discrimen to curve down to the furca base, as in moths and skippers, so one can hypothesize that it grew straight back in the mesothorax in the Pap.-Pier. line (perhaps twice, after Baroniinae evolved and in Pieridae) and in the Nym.-Lib. line. But it seems

more probable that the discrimen grew straight back in the mesothorax only once, in the Papilionoid ancestor (and in the metathorax of *Pseudopontia* the same thing occurred), and then in the Lycaenid ancestor (and slightly in *Baronia*) it curved down again, owing to the activation of metathorax genes.

The mesothorax anepisternum undergoes numerous changes, clearly independently. It is very large in moths and skippers, but became smaller in the Papilionoidea ancestor, and subsequently was frequently lost (by most Papilionidae, all Pieridae, the Danainae-Ithomiinae and Apaturinae-Nymphalinae-Acraeinae among the Nymphalidae, all Libytheidae, and most Lycaeninae of the Lycaenidae). The patagia has undergone many changes also. It is large in moths, skippers, Nymphalidae, and undoubtedly in the Papilionoidea ancestor, but was almost completely lost in Papilionidae and Libytheidae, in all Pieridae except Coliadinae, and lost in all Lycaenidae. This may represent as many as seven or more independent losses. The parapatagia seems to be another case of reversal. It is large and sclerotized in moths and skippers, but membranous in all Papilionoidea, except it has at least a trace of sclerotization in Charaxinae (and *Stibochiona* of Nymphalinae). It is much simpler to assume that this structure has become resclerotized in these two groups than to assume that it has been lost the eight or more times required by the hypothesis that Charaxinae retained it in an unbroken lineage from its moth ancestor. However, if the patagia could be lost numerous times, perhaps the parapatagia could be too.

The size of the male foreleg in the Lycaenidae seems rather conclusively to have reversed itself during evolution (Eliot, 1973; see Evolution of Lycaenidae). The ancestor of Lycaenidae (and Nym.-Lib.) probably had a five-segmented clawed male foretarsus, but it usually degenerated, and at least some Theclini later regained a larger segmented clawed male foreleg perhaps by using female (or pterothorax) genes. The arolium and pulvilli have also been lost independently (in Papilionidae, some Pieridae, some Nymphalidae (some Danainae and Nymphalinae, most Acraeinae)), and the pulvilli have become single in Pieridae and Lycaenidae. The claws often have become forked independently as well (in Pieridae, some Papilionidae, Nymphalidae (Acraeinae), Lycaenidae (Aphnaeini), and Hesperiidae (*Epargyreus*)).

The wing veins have undergone many changes, including the well-known branching of the R veins. The R veins of Pieridae often became stalked from each other, independently (Klots, 1931) of similar evolution in Nymphalidae. The tiny CuP vein (the "Cu-V cross-vein" of Ehrlich, 1958b; Cu_1 and Cu_2 of most U.S. authors actually represent veins CuA_1 and CuA_2, see Zeuner, 1943) present in Papilioninae (and as a rudiment in Heliconiini, etc. also) seems to be an advanced trait in adults. It is present in all Lepidoptera pupae, so is rather easily transferred to adults. A similar character is vein 1A+2A (commonly called vein 2A, see Zeuner, 1943). On the forewing these two veins usually join together at the base, forming one vein 1A+2A, but in Papilionidae they diverge. Because the veins are separate in the pupa, this is a simple derived feature.

"Secondary" setae (see Hinton, 1946) on first-stage larvae have developed independently several times, in Papilionidae, Lycaenidae, and in a few Nymphalidae (the Danainae, Morphinae, some Charaxinae; and some Nymphalinae, namely all Argynnini except *Euptoieta*).

Other characters with multiple changes are discussed by Ehrlich (1958b), and in

the "Origin of Pieridae" and "Origin of Lycaenidae" sections above. In general these are assumed to be due to parallel variation or reversal during evolution, as there is no way to arrange the butterfly family tree to eliminate problem characters.

Useless Characters

Some characters are very weak or useless. The "pilifers" on pupae (Mosher, 1916), which supposedly characterize Hesperioidea, Papilionoidea, Pyraloidea, etc., are not pilifers at all and should probably be called mandible remnants. True pilifers are tiny on adults, and absent in larvae, so one would not logically expect pupae to have large pilifers. Mosher's "gena" represents the orbit of the eye, often called the "smooth eyepiece." The secondary sclerite on the metascutellum cited by Brock (1971, p. 66) as present in Pieridae, Nymphalidae, and Lycaenidae, also seems useless. I examined all the families for this trait and could not find it in any, nor did Ehrlich (1958b). It is not demarcated by either a sulcus or a membranous area. Ehrlich (1960) and Miller (1971) list a "temporal suture" on the Hesperiid head, but, judging from the position of this sulcus, it is really the paratemporal sulcus, as suggested by Ehrlich (1960) himself, so there is no difference between skippers and Papilionoidea in this trait.

Several genital muscles studied by Stekol'nikov (1967) may provide useful characters when more complete studies are done: the "vaginal sclerite retractors and protractors" (=bursa dilators?), muscles to the membrane beneath the papilla analis, and the protractors of the aedeagus. Several generalizations made by Stekol'nikov are weakened by exceptions found by Arnold and Fischer (1977) and Ehrlich and Davidson (1961).

The "anterior sclerite" on the first abdominal sternite (sternum 2) was examined because Brock (1971, p. 66) suggested it might prove useful. I found much variation in it useful on the generic level, but probably not on the family level. In Hesperiidae this "anterior sclerite" is absent in *Epargyreus*, but an incomplete groove or small sulcus may indicate its presence in *Celaenorrhinus* (in which it is extremely wide, in front of diagonal scent pouches) and *Agathymus*. In Papilionidae a groove or small sulcus may indicate its presence in Baroniinae, but it is absent in *Parnassius* and apparently in *Papilio*. In Pieridae (*Ascia, Phoebis*) a wide sulcus delimits it. In Nymphalidae it is delimited by a weak groove in *Anaea*, a stronger groove in *Danaus* and *Precis* (and the Libytheidae), a lateral groove leading to a medial membranous cleft in *Oeneis, Asterocampa,* and *Speyeria*. In the Lycaenidae a slight lateral sulcus delimits the anterior sclerite only laterally in *Eumaeus* (which also has a median-transverse cleft) and *Pseudolycaena*. The anterior ventral lamina of the metathorax furca (Brock, 1971) is absent or vestigial in all skippers and butterflies, though perhaps present in *Epargyreus*. The furcal stem shows very little difference in length among butterflies and skippers. Brock's postfurcal sclerite, which is a continuation of the epimeron forward and down toward the furcal foot, is rather variable, extending to the foot in *Epargyreus, Baronia, Parnassius, Papilio, Phoebis,* and *Precis*, extending about to the furcal stalk in *Libytheana* and *Eumaeus*, and is nearly absent in *Agathymus, Ascia, Anteos,* and *Pseudolycaena*. A little-noticed trait is the hairlike dorsal bristles just above the claws, which show some variation, but most groups seem to have six bristles.

Kristensen (1976, p. 31) implies that Dismorphiinae and Pseudopontiinae lack hind tibial spurs. However, the legs I examined show this character to be weak. The

tibial spurs are small in Dismorphiinae and some Pierinae, large in Coliadinae and some Pierinae. The trait would seem to be useful in generic classification, but is oddly not mentioned by Klots (1931). Kristensen also states that "the lateralmost tergal muscle between II and III" is absent in Dismorphiinae and Pseudopontiinae, and cites Ehrlich and Ehrlich (1963) as the source of this; however, I cannot find this character in the Ehrlichs' paper, and believe there must be some mistake.

Discussion

The evolutionary origin of the families presented as Figure 3 appears reasonable, because many robust derived traits support the monophyly of its branches. Another tree produced by intuitive analysis of adult morphology (Ehrlich, 1958b) is essentially the same except for a slight difference in the origin of Lycaenidae and a few differences within Nymphalidae (the positions of Charaxinae and Calinaginae were reversed there due to a misprint). A computer analysis of 196 external and internal morphological traits (the "distance" tree of Ehrlich, 1967) provided results compatible with the present tree (where two taxa join another line at nearly the same point in the distance tree, one cannot have confidence in their origin). Kristensen's (1976) cladistic analysis produced different results, but the present paper, based on the same cladistic methods but using a larger data set, shows Kristensen's conclusions regarding the origin of Pieridae and Libytheidae unwarranted.

One difficulty in the use of phenetic methods for the study of evolution of a group is that some groups change characteristics at a faster rate than do others. This confuses the phenogram such that the slowly-evolving taxa are grouped together, and the rapidly-evolving taxa are placed on their own branches. Among the butterflies, the Papilionidae and Lycaenidae may have evolved faster than other families (Ehrlich, 1958b notes that Papilionidae have a greater percentage of derived adult characters, and Lycaenidae certainly have the most derived characters of larvae, pupae, and eggs), so they have often been given exaggerated status in phenetic classifications (Ehrlich, 1967), being positioned farther down the trunk of the tree, while the Pieridae, Nymphalidae, and Libytheidae have been grouped together merely because they evolved slower. Also, the Pseudopontiinae among the Pieridae, and the Acraeinae among the Nymphalidae, have evolved many freakish traits (as if they have been through a "genetic bottleneck" of inbreeding in one very small population), which have exaggerated their status in the phenogram of their families as well. Nevertheless, phenetic classifications may be useful for special purposes, such as judging whether a monophyletic taxon (as determined by cladistic or genetic methods) should be treated as a family or subfamily.

Likewise, our knowledge of the phylogeny of the subfamilies of Papilionidae is sound, based on the work of Munroe (1961), Munroe and

Ehrlich (1960), Ehrlich (1958b), and Hancock (1983), although there is some uncertainty regarding the validity and origin of the tribes. Knowledge of the phylogeny of Pieridae subfamilies is sound also, thanks to Klots (1931), Ehrlich (1958b), and Geiger (1981), although a tribal classification has not been attempted.

However, the classification of Nymphalidae needs more study, as there is some controversy about the division between Satyrinae and Morphinae, and between Charaxinae-Apaturinae-Nymphalinae-Acraeinae, and the precise origin of Calinaginae is based on rather few characters. A search for new characters is needed in Nymphalidae, and some larval and behavioral traits need to be ascertained in some groups. The tribes of Nymphalinae need to be studied, because this is the most diverse subfamily. The results may affect the status of Acraeinae, Apaturinae, and perhaps Charaxinae. The Lycaenidae also need more study, as the relationship of the subfamilies and of several tribes of Lycaeninae is controversial. The tribes of Riodininae are also uncertain and the Hesperiidae have certain problems. The relationship between the Hesperiinae and Trapezitinae needs to be clarified, and the phylogenetic relationship between Pyrginae, Coeliadinae, and Pyrrhopyginae must be studied (it is possible that the latter two subfamilies are merely phenetically extreme offshoots of a polyphyletic Pyrginae). A tribal classification of Hesperiidae is needed, as the current system seems weak.

Family vs. Subfamily Status.

Whether a subfamily is treated as a family or vice-versa is mainly a matter of philosophy, provided that principle #2, that each taxon must be monophyletic, is not violated. However, one can also use the degree of uncertainty of classification to help decide. For instance, the Riodininae and Lycaeninae (plus the Styginae) share numerous unique derived traits that distinguish them from other butterflies (see Lycaenidae) and there is no doubt whatsoever that they together form a monophyletic group, although they are sometimes treated as separate families. However, the subfamilies have a paucity of unique derived traits that would support their monophyly, and Eliot (1973, pp. 460-461) hinted that "all Riodininae may not be descended from one single ancestor and all Lycaenidae from another". The removal of Curetinae from Lycaeninae largely remedies this problem. Such uncertainty by an author of a higher classification of the Lycaenidae demands that we should treat these groups as subfamilies, because only the lumped family Lycaenidae promises stability.

A similar argument can be advanced for the family Nymphalidae, because the component subfamilies are a bit unsettled regarding how previous authors have treated their taxonomic affinity and their status. Thus the Ithomiinae have been considered close to Satyrinae (a treatment refuted by Gilbert and Ehrlich (1970)); some of the tribes included in Morphinae by Ehrlich (1958b) and the present paper were transferred to

Satyrinae by Miller (1968) while Vane-Wright (1972) transfers certain Satyrinae to Morphinae; the position of Calinaginae has been obscure; and the status of Apaturinae (as a member of Nymphalinae or even as a separate family) and its connection to Charaxinae has been shuffled about. Other Nymphalid taxa have been elevated to subfamilies or even families, such as Heliconiidae, "Marpesiinae", etc. Only the inclusive family Nymphalidae has had relative stability. While I am reasonably satisfied with the subfamily tree in Figure 3, there is a bit of a shortage of robust characters.

Actually the same argument could be advanced for treating Libytheidae as a subfamily of Nymphalidae, because Kristensen (1976) asserts that Libytheidae evolved from a Nymphalid, so must be a subfamily of Nymphalidae. However, the facts suggest that Libytheidae evolved from the Nymphalid root before the Nymphalidae evolved, so the treatment of Libytheidae is merely a matter of lumping or splitting.

The phenetic distance between subfamilies and families should also be used to define their family or subfamily rank. Probably because of the large number of species of Nymphalidae and Lycaenidae, these families have been divided into numerous weakly-defined "families." If splitting the families of Figure 3 is attempted, certainly the primary division of Hesperiidae would be one of the first to be recognized, as Pyrgidae and Hesperiidae. Baroniidae, Parnassiidae, and Papilionidae would have to be recognized, as well as Dismorphiidae, Pseudopontiidae, and Pieridae. Such splitting would then carve Stygidae from Lycaenidae, and Danaidae (including Ithomiinae) from Nymphalidae, but the Riodininae, Curetinae, Calinaginae, Satyrinae-Morphinae, Megathyminae, etc. would attain family rank only after a second round of splitting in which many subfamilies are raised to families. Such splitting seems rather pointless (who really cares whether a *d* replaces an *n* in the scientific name?), and Ehrlich is correct in attempting to make the butterfly families comparable to the families of beetles and microlepidoptera, even Noctuidae (which now contains the old families Notodontidae, Agaristidae, Pericopidae, etc.), and to make family names comprehensive enough so that the average entomologist can recognize them. Indeed on various grounds it can be argued that Ithomiinae should be lumped into Danainae, Coeliadinae and perhaps Pyrrhopyginae lumped as subgroups of Pyrginae, Acraeinae lumped into Nymphalinae, and Libytheidae perhaps lumped as a subfamily of Nymphalidae.

Pyrrhopyge araxes (Pyrrhopyginae), and Carla Maria Penz provided first instar *Actinote carycina* (Acraeinae).

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Butterflies of the California Channel Islands

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Abstract. The butterflies (Lepidoptera: Papilionoidea and Hesperioidea) of the eight California Channel Islands are listed, with indication of residency status. Generally, the island faunas are depauperate aggregations of mainland species. The short geologic duration of isolation and high vagility of most of the species have limited endemism. A species/area relationship exists, but turnover in species composition over time (and thus MacArthur-Wilson equilibrium) is difficult to document with available data.

Introduction

The California Channel Islands are a group of eight continental islands, ranging in area from 2.6 to 249 km², located 20 to 98 km off the coast of southern California. This preliminary compilation includes butterfly data from recent fieldwork, museum collections, and the meager literature. Further fieldwork and analysis are necessary to complete knowledge of faunal composition and affinities. Fieldwork is difficult due to limited accessibility of several of the islands and island weather conditions, which include regular strong winds and dense fog.

The eight California Channel Islands (Fig. 1) fall naturally into two groups: four northern (San Miguel, Santa Rosa, Santa Cruz, and Anacapa Islands) and four southern (Santa Barbara, San Nicolas, Santa Catalina, and San Clemente Islands). During the Middle Pleistocene, most of the islands were submerged, and perhaps only Santa Catalina and the higher parts of Santa Cruz and Santa Rosa Islands remained above water (Johnson, 1978, 1983). During the Late Pleistocene, the northern islands were united into one large island by eustatically lowered sea levels. A Late Pleistocene land bridge to the northern islands has long been hypothesized, but neither geological nor biological evidence support a mainland connection since Early Pleistocene or before (Johnson, 1978). No connections existed among the southern islands during the Late Pleistocene. Therefore, the biotas of most of the islands have arisen since Middle Pleistocene times. For background information, see Miller (1984a), Miller and Menke (1981), and Power (1980).

Except for Santa Catalina Island, the islands have been surveyed for insects only by visiting entomologists. The butterflies of Santa Catalina
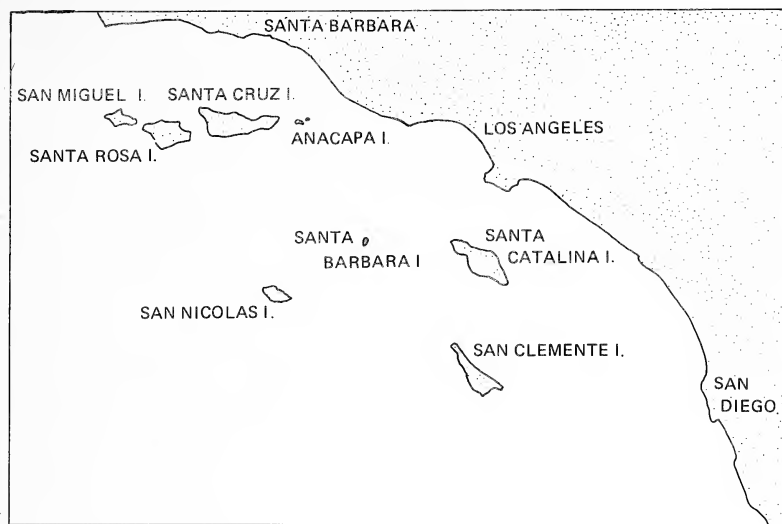
Fig. 1. California Channel Islands.

Island were treated by Meadows (1937, including description of *Antho-charis cethura catalina*), who lived on the island from 1927 to 1934. The only other island treatment is for Santa Cruz Island (Langston, 1981). Wright (1905) described the Santa Catalina Island endemic *Strymon avalona* (as *Thecla avalona*), and Ingham (1933) described *Anthocharis sara gunderi* from the same island. Emmel and Emmel (1975) described *Euphydryas editha insularis*, endemic to Santa Rosa Island. Other references to island butterflies include: Bowers (1890), Burns (1964), Cockerell (1938a, 1938b, 1939, 1940), Comstock and Dammers (1933), Coolidge (1923), Emmel and Emmel (1973), Evans (1955), Gall (1981), Goodpasture (1973), Gorelick (1971), Grinnell (1909), Hovanitz (1941, 1950, 1962), LeGare and Hovanitz (1952), Orsak (1976), Powell (1981, 1984), Remington (1971), Scott (1981), and Thorne (1970). Island butter-flies are scattered throughout many collections; Principle sources of material are the Natural History Museum of Los Angeles County (LACM), Santa Barbara Museum of Natural History (SBMNH), California Insect Survey (University of California at Berkeley, CIS), and Peabody Museum of Natural History (Yale University); smaller amounts of material are in National Museum of Natural History (Smithsonian Institution, USNM), San Diego Natural History Museum, University of California at Davis, and other institutions.

Distribution Data

Table 1 lists the butterflies recorded from each of the islands, with

indication of the status of the island populations. Names generally follow Emmel and Emmel (1973). Resident (reproducing) populations are indicated by the abundance and quality of specimens, as well as records of immatures. Some species (e.g. *Vanessa* species) probably migrate regularly between the islands and the mainland, occasionally breeding, but not always maintaining permanent populations. See appendix for comments on taxonomic or residency status of some taxa.

Ecological Biogeography

Like most island organisms, the butterfly faunas of the California Channel Islands are depauperate compared to the adjacent mainland. Santa Cruz Island, with 34 species, has the largest butterfly fauna of the islands. This is less than half that of a region of equivalent area and elevational range on the adjacent coastal Santa Barbara region, which has about 70 resident butterfly species (Table 2). Possible reasons for this lack of island butterfly diversity include: (1) poor dispersal abilities of some butterflies due to limited vagility, (2) low habitat diversity and lack of or scattered, patchy presence of foodplants on the islands, (3) competitive displacement by other butterfly species, (4) physiological limitations of certain butterflies, and (5) destruction of original habitats by human activities.

Linear regression of number of species of butterflies against island areas yields a significant correlation (r=.83), with the following equation: species=7.3 + (.078) (area). Maximum elevation and number of plant species are also strongly correlated with number of butterfly species (Miller, ms). Butterfly numbers are remarkably similar to those of Orthoptera, the only other well surveyed group of insects on these islands (Table 3).

Many authors have used the existence of a species/area relationship to claim occurrence of MacArthur-Wilson equilibrium. This theory (MacArthur and Wilson, 1967) states that the number of species of a given higher taxon on an island is a function of rates of immigration and extinction, which in turn are dependent on area and isolation. However, demonstration of application of this model requires that (1) a relationship exists between number of species and area, (2) the number of species remains constant, and (3) the species present turnover with time due to extinction and immigration (Gilbert, 1980). Characterization of status of residency is difficult due to the problems in defining "colonization" and "extinction" (Simberloff, 1976), especially with the limited data available and the "weedy" nature of many of the species involved (which often have no "permanent" populations, but only ephemeral local "populations" which are regularly reestablished; Shapiro, 1982). Demonstration of turnover in California Island butterflies is difficult due to lack of adequate census data, especially over time.

In comparing Santa Catalina Island butterflies surveyed by Meadows (1937) from 1927-1934 with recent (1968-1981) collections (LACM, CIS, SBMNH), the number of species has remained approximately constant. During each period the apparent establishment or reestablishment of a species associated with cultivated plants has occurred: *Phoebis sennae* in 1928 and *Strymon melinus* (not restricted to cultivated plants) in 1978. Among other species, *Eurema nicippe* (associated with cultivated plants), *Danaus gilippus strigosus* (a migrant), and *Nymphalis californica* (a migrant) were taken only in the early period; *Junonia coenia* and *Plebejus acmon* only in the recent period. Thus some turnover may have taken place, but the breeding status of many of these species is not known and isolated populations could have been missed on this large, rugged island.

On Santa Cruz Island, although lack of data prevents comparisons of entire groups through time, Powell (1981) documented that an earwig, two moths and two butterflies not recorded in 1939-41 and 1966-69 surveys, became established during 1969-78. A third butterfly, *Atalopedes campestris,* is added herein (appendix). The earwig and moths were probably introduced by man, but the sudden appearance of the butterflies is not easily interpreted. They might have immigrated often during the 50-100 years Santa Cruz Island has had their weedy hostplants. Such species probably periodically colonize, are eliminated during stress such as over-grazing by feral sheep in drought years, then recolonize. Powell (1981, 1984) suggests that the insect faunas of the California Channel Islands, especially the badly perturbed ones, are undersaturated and have not yet established (or reestablished) equilibrium species numbers. Extinction presumably is (or has been) higher than normal, immigration lower, and/or colonization improbable due to reduced patch sizes of native hostplants.

The butterfly fauna of Santa Catalina Island is the best known of the California Islands due to the relative intensity of collecting there. The faunas of San Nicolas and San Clemente, both smaller and more isolated than Santa Catalina, are poorly known; isolation and limited habitat diversity are responsible for the small numbers of species, but the presently known faunas are undoubtly incomplete. The fauna of the tiny and isolated Santa Barbara Island appears to be fairly well known; this island has little habitat diversity and has suffered greatly from human disturbance (Philbrick, 1972). The fauna of Santa Cruz Island is well known, due especially to fieldwork by R. L. Langston, J. A. Powell, and C. L. Remington. The large size and topographic diversity of this island provides greater habitat diversity than any of the other islands. Anacapa Island (actually composed of three islets) appears to have a large fauna for its small size. This may be due to its proximity to both Santa Cruz Island and mainland sources of immigrants. The faunas of Santa Rosa and San Miguel Islands are poorly known due to incomplete collecting, but both are smaller and considerably less diverse in vegetation and topography than

Santa Cruz. Several of the islands, especially San Miguel, have suffered considerable overgrazing in the past (Johnson, 1980).

Historical Biogeography

Butterflies show little phenotypic endemism on the California Islands, although many individuals tend to be somewhat smaller and darker than those on the mainland, probably due largely to climatic factors (Hovanitz, 1941). Morphological variation in very few populations is significant and constant enough to warrant specific or subspecific status: *Anthocharis sara gunderi, Anthocharis cethura catalina, Cercyonis sthenele* new subspecies, *Euphydryas editha insularis, Strymon avalona,* and *Ochlodes sylvanoides santacruza.* Allozyme and karyotype frequencies of the fly *Drosophila pseudoobscura* Frolova from the California Islands do not differ much from those of mainland populations, indicating that isolation does not necessarily lead to genetic differentiation (Harshman and Taylor, 1978), although it can (Weissman, 1976).

Some butterfly populations on the islands differ considerably in phenology and/or abundance from mainland populations. On the islands *Ochlodes sylvanoides* flies from spring into summer (late April to August), apparently having shifted its later flight period on the mainland to replace that of *Ochlodes agricola* (Boisduval) which does not have insular populations; on the mainland, *O. agricola* flies in spring (May to June) at the same localities that *O. sylvanoides* occupies in the summer (June to September). The prolonged flight periods of several species are evidently due to the coastal climate with mild winters and cool summers (Langston, 1975) and reduced competition from related species which are absent on the islands. In one case, related species are found on adjacent islands but do not occur together: *Euphydryas editha insularis* is locally abundant on Santa Rosa Island and *E. chalcedona* is locally abundant on Santa Cruz Island, but neither island has both species.

Development of endemism has been limited by the high vagility of many species and the short geologic duration of isolation. Many of the island butterflies (e.g., *Pieris protodice, P. rapae, Colias eurytheme, Vanessa atalanta rubria, V. cardui, V. annabella, V. virginiensis, Junonia coenia, Strymon melinus, Lycaena helloides, Brephidium exilis, Plebejus acmon acmon, Hylephila phyleus, Pyrgus albescens,* and others) are common lowland colonizers elsewhere in California (e.g., Shapiro, 1975, 1980, 1982). The biotas of most of the California Islands must have arisen since the last submergence in the Middle Pleistocene (Johnson, 1978). The time since initial colonization (which may have taken place anytime since the last submergence) probably has not been long enough to allow significant morphological divergence on the islands. The fossil record is inadequate to document the morphological stability of butterflies during the Pleistocene (Shields, 1976) but the known Pleistocene butterflies (one papilionid, one

pierid, one nymphalid, and two hesperiids) are considered to be extant species (Zeuner, 1942, 1962; Fujiyama, 1968). Analysis of Pleistocene insect fossils, primarily beetles, from various Holarctic localities indicates great morphological stability of species from the Pleistocene through the present (Ashworth, 1979; Coope, 1979; Matthews, 1977; Miller, 1983). Furthermore, during the Late Pleistocene glaciations, the northern islands were united into one island (Johnson, 1978). For most butterflies, the duration of isolation on these islands has not been long enough to allow evolution of endemic taxa. Isolation has been limited by both geologic processes and vagility of the butterflies, some of which can easily cross the water barriers involved. Some of the island endemics may be relicts of taxa which were more widespread during the Pleistocene.

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Appendix. Notes on the taxonomic or residency status of certain island butterfly taxa.

Colias harfordii: The Santa Cruz Island specimens are assumed to be this, but the classification of mainland *harfordii* is still uncertain (e.g. Ferris, 1973; Klots, 1975). *Eurema nicippe* and *Phoebis sennae*: Once resident on Santa Catalina Island only at Avalon, where their introduced foodplant, *Cassia* species (Leguminosae), is cultivated (Meadows, 1937); no recent records.

Anthocharis cethura catalina: The restriction of the type locality to "ridge between Renton Mine and Jewfish Point at head of Pebbly Beach Canyon" by L. Miller and Brown (1981:75) is unnecessary since (as noted by Orsak, 1976) the holotype was collected at Grand Canyon and is so labelled.

Anthocharis sara gunderi: Although *gunderi* is considered a synonym of *sara sara* by some authors (Meadows, 1937; L. Miller & Brown, 1981), the Catalina population is as differentiated from *sara sara* as are the mainland *sara* subspecies (J.F. Emmel, pers. comm.). The Santa Rosa and Santa Cruz populations are, however, referable to *sara sara*.

Cercyonis sthenele: The Santa Cruz Island population is an undescribed endemic subspecies (C. L. Remington and J. F. Emmel, pers. comm.).

Agraulis vanillae incarnata: Occurs only where its introduced foodplant, *Passiflora* species (Passifloraceae), is cultivated on Santa Catalina Island (Powell, 1984).

Euphydryas editha insularis: The subspecific characters, described (Emmel & Emmel, 1975) from six specimens collected in 1941, are consistent in a series collected at many localities on Santa Rosa Island in April 1976 (SBMNH).

Vanessa cardui: "A north-westerly flight of hundreds of specimens was observed on San Clemente between November 23 and 26, 1939. During the flight Dr. John Garth, on board the... *Velero III*, saw two specimens on the wing seven miles [11 km] off the northern end of the island" (D. Meadows, unpubl. notes at LACM).

Strymon melinus: Resident on all islands except Santa Catalina, where it evidently occsionally establishes temporary local populations (1918, 1978-1982).

Celastrina argiolus echo: Grinnell's (1909) record of "*Cyaniris pseudoargiolus piasus*" from San Clemente Island is probably this. Meadows (unpubl. notes) recorded *echo* from San Miguel Island, but since I have been unable to locate specimens, I consider this a misidentification of *Everes amyntula*.

Ochlodes sylvanoides: Scott (1981) has recently described the Santa Cruz Island population as *O. sylvanoides santacruza*, without consideration of other island populations. This name is unfortunate in view of the variability and taxonomic problems in *Ochlodes* (e. g. Tilden, 1975).

Atalopedes campestris: Three males collected in the Central Valley of Santa Cruz Island, in the field just west of the University of California Field Station, 22-29 June 1979 (C.D. Nagano: LACM), represent a new island record. Dornfield (1980:109) records the recent range expansion of this species into Oregon.

Erynnis funeralis: Burns(1964:133) suggested that Meadows' (1937:180) record of *E. tristis* from Santa Catalina Island actually applied to *E. funeralis* but had not seen the specimen. He has recently seen the specimen (and two others from Catalina, all in LACM) and confirms the *funeralis* identification (J. M. Burns, pers. comm.). The San Clemente Island record is based on 1 male collected at West Cove, 21 March 1972 (H.V. Daly: CIS).

Table 1.   Butterflies of the California Channel Islands. Abbreviations: R=resident; I=resident, but dependent on introduced ornamental plants; S=stray (accidental occurrence); X=status undetermined (includes regular migrants).

	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island(s)	Santa Barbara Island	Santa Catalina Island	San Nicolas Island	San Clemente Island
PAPILIONIDAE								
Papilio zelicaon Lucas		X	R			R		R
Papilio eurymedon Lucas			R					
PIERIDAE								
Pieris protodice Boisduval & LeConte		R	R		X	R	R	R
Pieris rapae (Linnaeus)			R			R		X
Colias eurytheme Boisduval		R	R	R	X	R	R	X
Colias harfordii Henry Edwards			R					
Eurema nicippe (Cramer)	S					I		
Phoebis sennae (Linnaeus)						I		
Anthocharis cethura catalina Meadows						R		
Anthocharis sara gunderi Ingham						R		
Anthocharis sara sara Lucas		R	R					
NYMPHALIDAE								
Danaus plexippus (Linnaeus)	X	R	X	X	X			
Danaus gilippus strigosus (Bates)						S		
Cercyonis sthenele subspecies			R					
Agraulis vanillae incarnata (Riley)						I		
Speyeria callippe (Boisduval)			R					
Euphydryas c. chalcedona (Doubleday)			R					
Euphydryas editha insularis Emmel & Emmel	R							
Chlosyne gabbii (Behr)			R	R				
Nymphalis a. antiopa (Linnaeus)	X	R				R		
Nymphalis c. californica (Boisduval)						S		
Vanessa atalanta rubria (Fruhstorfer)			R	X		R		

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	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island(s)	Santa Barbara Island	Santa Catalina Island	San Nicolas Island	San Clemente Island
Vanessa cardui (Linnaeus)	X	R	R	X	X	R	X	R
Vanessa annabella (Field)		R	R	R	R	R	R	R
Vanessa virginiensis (Drury)		R	R	R		R	X	R
Junonia coenia Huebner		X	R	X		R		
Adelpha bredowii californica (Butler)			R					
LYCAENIDAE								
Strymon avalona (Wright)						R		
Strymon melinus Huebner	R	R	R	R	R	X	R	R
Satyrium s. saepium (Boisduval)			R					
Callophrys d. dumetorum (Boisduval)			R					
Lycaena helloides (Boisduval)			R					
Leptotes marina (Reakirt)			X	X		R		
Brephidium exilis (Boisduval)	R	R	R	R	R	R	R	R
Everes a. amyntula (Boisduval)	R	R	R	R		R	R	
Plebejus a. acmon (West. & Hewit.)		R	R	R		R	R	X
Glaucopysche lygdamus australis Grinnell		R	R					
Celastrina argiolus echo (Edwards)		X	R			R		R
HESPERIIDAE								
Ochlodes sylvanoides (Boisduval)		X	R			R		
Atalopedes campestris (Boisduval)			R					
Polites s. sabuleti (Boisduval)	R	R	R	R				
Hylephila phyleus (Drury)	X					R		
Pyrgus albescens Ploetz		R	R	X	X	R	R	
Erynnis t. tristis (Boisduval)			R					
Erynnis funeralis (Scudder & Burgess)							X	X

Table 2. Butterflies of the Santa Barbara-Goleta coastal shelf and adjacent Santa Ynez Mountains, Santa Barbara County, California. Data from museum collections (especially Santa Barbara Museum of Natural History), private collections, and literature. Asterisk (*) indicates taxa not resident, or dependent on ornamental plants.

PAPILIONIDAE

Papilio zelicaon Lucas
Papilio rutulus rutulus Lucas
Papilio eurymedon Lucas

PIERIDAE

Pieris protodice Boisduval & LeConte
Pieris rapae (Linnaeus)
Colias eurytheme Boisduval
Colias harfordii Hy. Edwards
Colias eurydice Boisduval
*Phoebis sennae marcellina (Cramer)
*Eureme nicippe (Cramer)
Nathalis iole Boisduval
Anthocharis sara sara Lucas
Anthocharis lanceolata australis
  (Grinnell)

NYMPHALIDAE

Danaus plexippus (Linnaeus)
*Danaus gilippus strigosus (Bates)
Coenonympha california california
  (Westwood)
Cercyonis sthenele (Boisduval)
*Agraulis vanillae incarnata (Riley)
Speyeria callippe (Boisduval)
Euphydryas chalcedona chalcedona
  (Doubleday)
Euphydryas editha (Boisduval)
Chlosyne gabbii (Behr)
Thessalia leanira (Felder & Felder)
Phyciodes pratensis pratensis (Behr)
  [=P. c. campestris (Behr)]
Phyciodes mylitta mylitta (Edwards)
Polygonia satyrus satyrus (Edwards)
Nymphalis antiopa antiopa (Linnaeus)

*Nymphalis californica californica
  (Boisduval)
Vanessa atalanta rubria (Fruhstorfer)
Vanessa cardui (Linnaeus)
Vanessa annabella (Field)
Vanessa virginiensis (Drury)
Junonia coenia Huebner
Limenitis lorquini lorquini Boisduval
Limenitis bredowii californica
  (Butler)

LYCAENIDAE

Apodemia mormo virgulti (Behr)
Calephelis nemesis californica
  McAlpine
Atlides halesus estesi Clench
Strymon melinus Huebner
Satyrium californica (Edwards)
Satyrium sylvinus dryope (Edwards)
Satyrium auretorum spadix (Hy.
  Edwards)
Satyrium tetra (Edwards)
Satyrium saepium saepium
  (Boisduval)
Callophrys augustinus iroides
  (Boisduval)
Callophrys dumetroum dumetorum
  (Boisduval)
Lycaena arota (Boisduval)
Lycaena gorgon (Boisduval)
Lycaena helloides (Boisduval)
Leptotes marina (Reakirt)
Brephidium exilis (Boisduval)
Everes amyntula amyntula
  (Boisduval)
Plebejus acmon acmon (Westwood &
  Hewitson)

Euphilotes battoides bernardino (Barnes & McDunnough)
Philotes sonorensis (Felder & Felder)
Glaucopsyche lygdamus australis Grinnell
Celastrina argiolus echo (Edwards)

HESPERIIDAE

Panoquina panoquinoides errans (Skinner)
Lerodea eufala (Edwards)
Paratrytone melane (Edwards)
Ochlodes sylvanoides (Boisduval)
Ochlodes agricola (Boisduval)
Atalopedes campestris (Boisduval)
Polites sabuleti sabuleti (Boisduval)
Hylephila phyleus (Drury)
Pholisora catullus (Fabricius)
Heliopetes ericetorum (Boisduval)
Pyrgus albescens Ploetz
Erynnis funeralis (Scudder & Burgess)
Erynnis tristis tristis (Boisduval)
Erynnis propertius (Scudder & Burgess)

Species recorded from the Santa Barbara area which are not residents or regular migrants:

PAPILIONIDAE

Papilio indra pergamus Hy. Edwards: The stated type locality, "near Santa Barbara" is evidently erroneous (Miller, 1984b).
Battus philenor hirsuta (Skinner): 1, Santa Barbara, 11 April 1911 (J.A.

Comstock: LACM); 1, Carpinteria, 11 August 1956 (N.W. Baker: SBMNH).

PIERIDAE

Phoebis agarithe agarithe (Boisduval): 1 male, Santa Barbara, 19 April 1917 (T. Lehmann: SBMNH); cited by Emmel and Emmel (1973:21).
Euchloe ausonides (Lucas): 1 male, "Santa Barbara, July 1911" (LACM). The locality and date are probably both erroneous (P.A. Opler, pers. comm.).

NYMPHALIDAE

Speyeria coronis (Behr): The specimens Emmel and Emmel (1973:30) reported from "near San Marcos Pass" (1 each in SBMNH and LACM, not collected by Lane) appear to be mislabelled *S. zerene* (Boisduval) (L.P. Grey, pers. comm.), and are erroneous records.

LIBYTHEIDAE

Libythena bachmanii larvata (Strecker): 1 male, Carpinteria, 29 December 1963 (D. Davenport: SBMNH).

LYCAENIDAE

Hemiargus isola alce (Edwards): 2 females, Montecito, June 1960 (SBMNH).

HESPERIIDAE

Thorybes pylades (Scudder): 1 female, San Marcos Pass, 22 March 1931 (C.W. Kirkwood: Yale).

Table 3. Numerical data. Butterfly numbers from Table 1, excluding "stray" records and species feeding only on cultivated plants. Orthoptera numbers from Weissman and Rentz (1976) with corrections for recent changes (Rentz and Weissman, 1982; D.B. Weissman pers. comm. 1984).

ISLAND	AREA (km²)	BUTTERFLIES	ORTHOPTERA
San Miguel	37	6	8
Santa Rosa	217	20	26
Santa Cruz	249	34	40
Anacapa	2.9	15	14
Santa Barbara	2.6	8	8
Santa Catalina	194	24	32
San Nicolas	58	10	10
San Clemente	145	12	11

A Second Phenotype of *Satyrium calanus* (Huebner) from Wyoming (Lepidoptera: Lycaenidae; Theclinae)[1]

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Abstract. A population of *Satyrium calanus* was discovered in north-eastern Wyoming in 1983. This population is dark-colored and relatively uniform in maculation in comparison to the highly variable pale phenotype discovered in 1977 in southeastern Wyoming. This new northeastern phenotype is discussed and illustrated.

Introduction

In 1983, the author was asked to assist the administration of Devils Tower National Monument in initiating a three-year insect resources survey within the confines of the park. This effort is part of an on-going program to inventory the natural resources in National Parks and Monuments throughout the United States. The Monument occupies a relatively small region and is nearly square, with an area of approximately 3.6 square miles (930 ha). The principal topographic feature is a magma intrusion in the center of the park which rises 867 feet (264 m) above its base, and 1267 feet (386 m) above the Belle Fourche River which passes through the southeastern portion of the park. The elevation of the river area is 3850 feet (1174 m) above sea level.

Vegetation types consist of mixed-grass prairie, oak and mixed deciduous forest, Ponderosa pine forest (*Pinus ponderosa* Laws.), and riparian flora along the river. Typical habitat is illustrated in Fig. 1. A single road serves the park headquarters and a visitor center. The environment is relatively undisturbed, except along the river.

The area has been protected since 1906 when President Theodore Roosevelt proclaimed the park as the first national monument under the Antiquities Act. Consequently pesticides have not been applied to the area, although some damage has occurred along the river bottom, especially to the Fremont cottonwoods (*Populus fremontii* S. Wats.) as a result of drift from aerial spraying of herbicides (picloram) over neighbor-
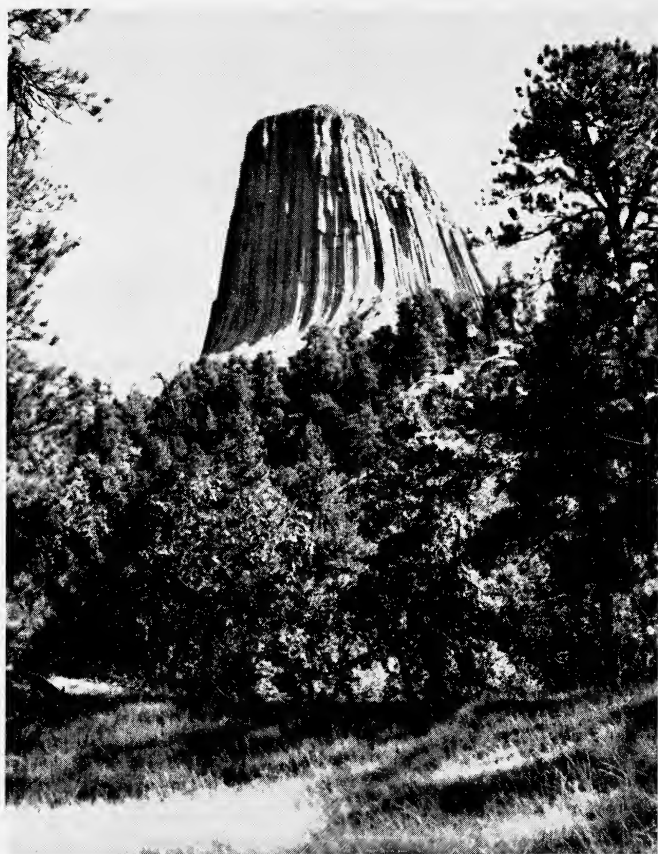
Fig. 1.   Devils Tower showing a typical collecting site in the oak-pine
transition belt.

ing ranch lands in an attempt to control leafy spurge (*Euphorbia
esula* L.).

   Wyoming is depauperate in oak, the larval host of *S. calanus*. Oak
occurs in two areas only in the eastern portion of the state, as indicated in
Fig. 2. Although there are a few reports in the literature that *Prunus* sp. is
utilized by *calanus*, oak is the favored host. Gambels oak (*Quercus gam-
belii* Nutt.) occurs in southern Carbon Co. in the SE portion of the state,
and Bur oak (*Q. macrocarpa* Michx.) is the species found in Crook Co.
where Devils Tower is situated. Although the oak forest extends beyond
the confines of the park to the north and eastward into the Black Hills,
calanus has not been recorded previously from this region of
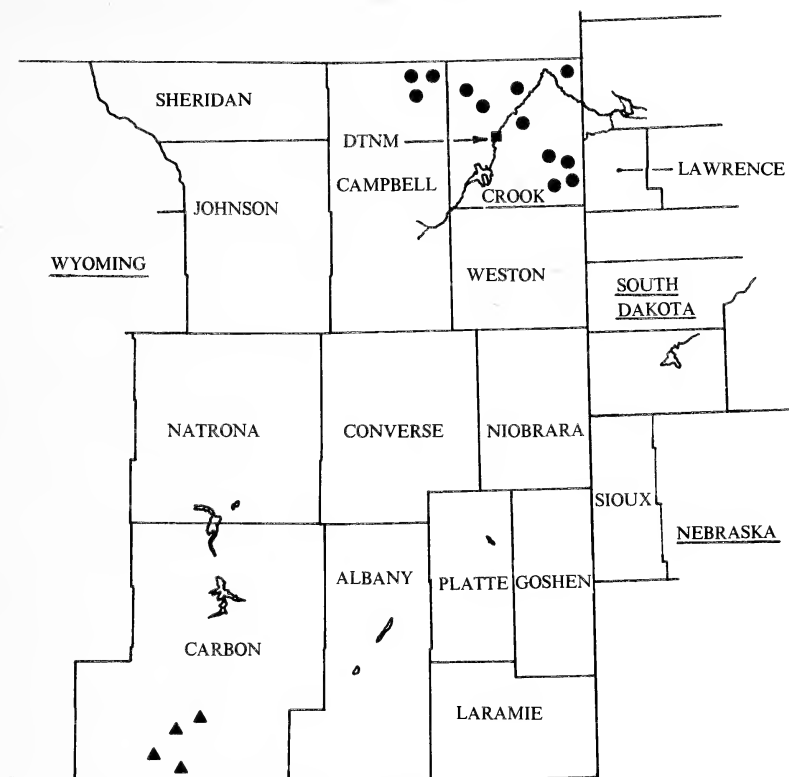Wyoming, and the only record from contiguous South Dakota is from

Fig. 2. Distribution of oak in Wyoming. Only the eastern portion of the state is shown since oak has not been recorded elsewhere. The dots represent *Q. macrocarpa* and the triangles *Q. gambelii*. Records are from the Rocky Mountain Herbarium, University of Wyoming.

Lawrence Co. It may be that *calanus* is particularly sensitive to some insecticides or herbicides, since for a number of years the general region surrounding the park has been treated with a variety of chemicals in an attempt to control various forest and agricultural pests.

The Crook Co. Phenotype

Two previous papers (Ferris, 1981[82], 1982[83]) discussed the distribution and phenotypes of *S. calanus* in the southern Rocky Mountains. The Front Range region from northern New Mexico to central Colorado supports populations of *S. calanus godarti* (Field), which is a very dark insect, both dorsally and ventrally. Along the Western Slope in Colorado through the Rabbit Ears Pass area and into Carbon Co., Wyoming, a very
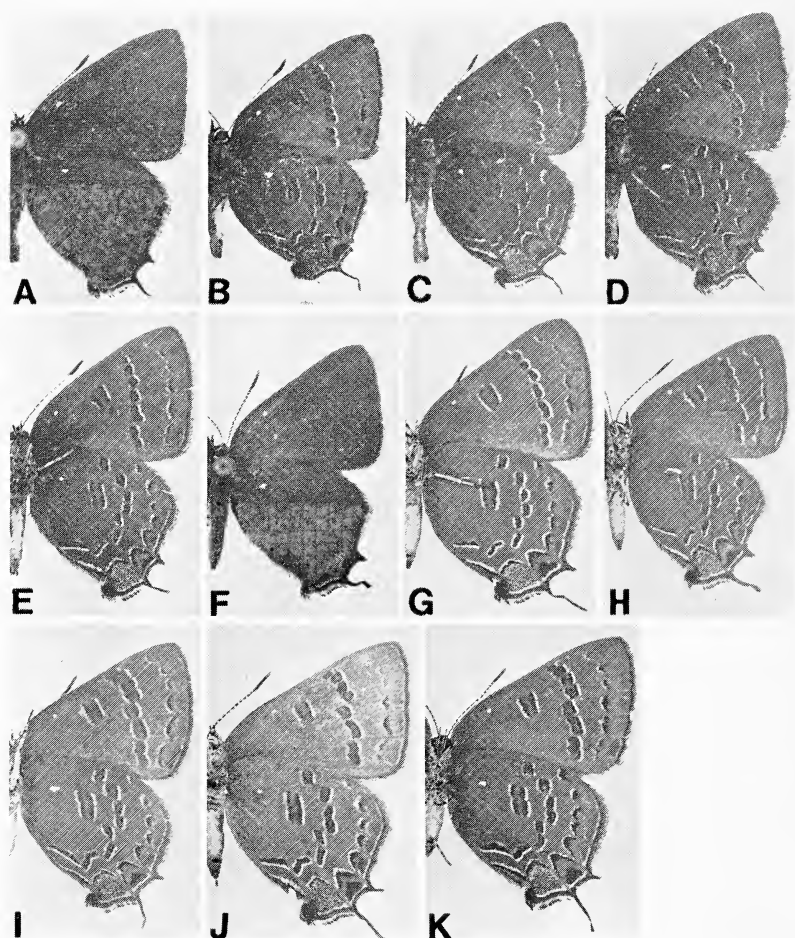
Fig. 3. Variation in *S. calanus godarti* from Devils Tower National Monu-
ment, Crook Co., Wyoming. All specimens were collected on 21-22
July, 1983. **A.** Male, dorsal. **B-E.** Males, ventral. **F.** Female, dor-
sal. **G-K.** Females, ventral.

pale phenotype occurs, with many individuals exhibiting the "heathii"
form as described in some detail by Fisher (1976) and Ferris (1982[83]).
Scott (1981) applied the name *albidus* to the Western Slope population,
but the validity of this taxon has been questioned (Ferris, 1982[83]).

Specimens from Devils Tower are not quite so dark dorsally as in typical
godarti, but rather are a paler and warmer brown. Ventrally they tend to
be a slightly warmer gray-brown than *godarti* from southern Colorado
and northern New Mexico. On the whole, however, they fit within Field's

original description of the taxon, especially with respect to the ventral markings and the orange color of the VHW submarginal lunules.

The Devils Tower specimens are rather uniform in their ventral markings. The main variation is in the extent of the orange lunules in the submarginal band on the hind wing. In some specimens, only two orange spots appear, while others have orange markings extending the entire length of the submarginal band. There is some degree of variation in the size, shape, and angle of the upper slash mark along the inner margin of the VHW. These characters are illustrated in Fig. 3. The width of the VFW mesial band varies to some extent, especially in the females.

Devils Tower material from Crook Co. contrasts markedly with specimens from Carbon Co., illustrated by Ferris in an earlier paper (1982[83]). Devils Tower specimens are dark colored and generally rather uniform in maculation. Carbon Co. specimens, on the other hand, manifest a considerable range of color variation and maculation. Although larval host may have some influence upon *calanus* phenotype, one cannot necessarily attribute the observed phenotypic differences to different species of larval host plants, since Front Range dark *godarti* and the Western Slope pale phenotypes both utilize *Q. gambelii*.

The geographic separation between the two Wyoming colonies of *calanus* is approximately 270 air miles (435 km). Adult emergence at Devils Tower occurs about two weeks prior to adult emergence in Carbon Co. The probable reason for this is the elevation difference between the two localities. The Carbon Co. site is about 3500 feet (1067 m) higher in elevation than the Devils Tower area.

A series of approximately 70 specimens of *calanus*, predominately males, was collected at Devils Tower. These were taken by the traditional method of beating the oak foliage and observing where the startled butterflies settled. Only a very few specimens were taken at nectar sources, and those were primarily leafy spurge plants. Collecting took place on broad "bench" areas above the Belle Fourche River where the major oak stands occur. The pine forest exists at a slightly higher elevation.

Sympatries

At the Carbon Co. colony site of *calanus*, *S. liparops aliparops* (Michener & dos Passos) is sympatric and commences its flight period 1-2 weeks prior to *calanus*. The same situation exists at Devils Tower. A few worn *S. liparops aliparops* were taken when *calanus* was at its peak on July 21-22, 1983. One specimen was taken while perching on oak, the others were in association with *Prunus* sp., and *Crategus* sp., both of which are reported larval hosts for this species. This is also the first record of *liparops* from Crook Co., although the species has been taken in Lawrence and Harding counties, South Dakota and Sioux Co., Nebraska.

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The Immature Stages of Six California *Catocala* (Lepidoptera: Noctuidae)

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Abstract. The traits of the ova, first instar larvae, second instar larvae, and fifth instar larvae that are shared by *Catocala andromache, C. benjamini, C. californiensis, C. chelidonia, C. johnsoniana* and *C. mcdunnoughi* are summarized. The ova and larvae of the six species are described. Keys for the separation of the first, second and fifth instar larvae are provided. The larvae are oak feeders.

Introduction

The early stages of six species of small California *Catocala* have not previously been published. The species are *Catocala andromache* Henry Edwards (1885), *C. benjamini* Brower (1937, 1982), *C. californiensis* Brower (1976), *C. chelidonia* Grote (1881), *C. johnsoniana* Brower (1976) and *C. mcdunnoughi* Brower(1937). In 1978 and 1979 I reared all six species from ova, and herein describe their life histories, provide keys to the immatures, and discuss the phyletic affinities of the species to each other.

Morphological Characters Common to all Six Species

Ova: In all species spheroidal, yellow or yellow-brown, with thin, flexible choria. Micropylar areas flattened, smooth, wide. From their edges descend 50 to 75 narrow, low, rounded, smooth ribs, these dividing initially or below, reuniting or joining an adjacent rib, disappearing basally. The micropylar ends of the ribs form low, polygonal rims around the micropyle. Ova diameters: from 1.02 mm to 1.29 mm (means).

Larvae: I use the terminology of Snodgrass (1928, 1935), Hinton (1946) and Hasenfuss (1963), in describing the larvae (schematic given in Figure 1).

First instar larva: (Figure 2) Significant features: head unicolorous, brown or black with black setae; cervical sclerites matching head. Body in pale colors, setae black, strong; from prominent, brown or black bases. Ventral setae short, white. Pattern in brown to black, and except in *C. mcdunnoughi*, browns darkening to black during the instar. In all species, three longitudinal lines on upper sides, their positions constant in relation to primary setae. Line 1, uppermost, from TI, through D2 setae of TII and TIII, and D1 and D2 setae of A1 to A8, on A9 passing dorsad of seta D1 to seta D2, ending, or to A10. Line 2, from TI, through SD2 setae of TII and TIII, through seta SD1 of A1, dorsad of SD1 setae on A2 to A9, to A10, on
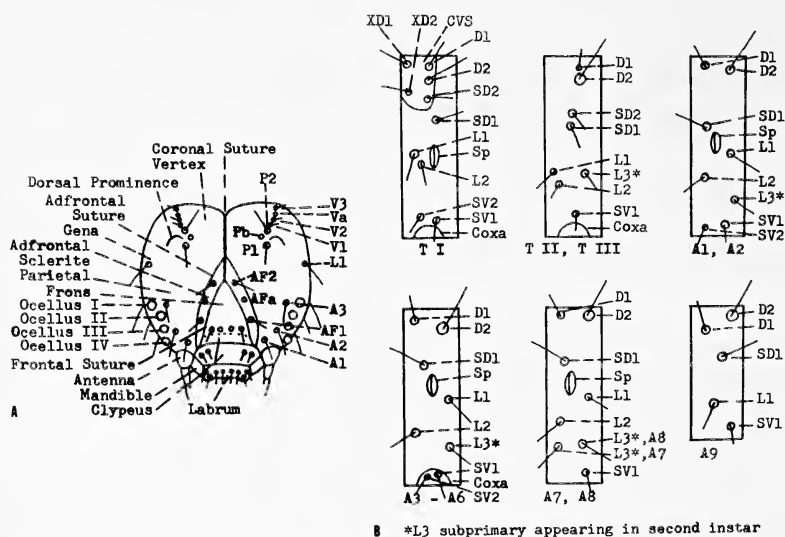
Fig. 1. **A.** Head regions, sutures, setae, and sensoria of *Catocala* larvae, dorso-frontal view. Setae with capital letters and arabic numerals; sensoria with capital letters and small letters; ocelli with Roman numerals. Only those referred to in the descriptions are designated. From reared *Catocala chelidonia* and *C. johnsoniana* larvae. **B.** Thoracic and abdominal setae of *Catocala chelidonia* and *johnsoniana* larvae. Only setae referred to in descriptions are shown. Segment 10 omitted.
Head: A - anterodorsal, AF - adfrontal, P - posterodorsal, V - vertex, L - lateral.
Body: CVS - cervical sclerite, XD - anterior dorsal tactile setae of TI, D - dorsal, SD - subdorsal, L - lateral, SV - subventral, Sp - spiracle, TI, TII, TIII - thorax; A1-A9-abdomen.

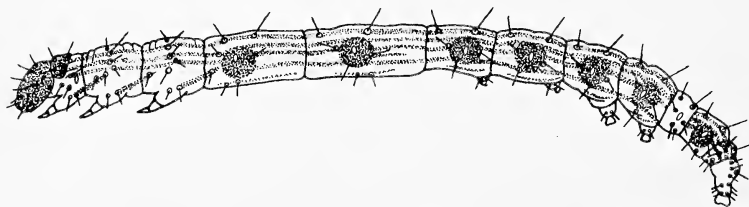Fig. 2. First instar larva of *Catocala benjamini*, in lateral view, length about 9.5 mm.

A9 often through seta D1. Line 3, from TI, near, or through SD1 setae of TII and TIII, and through SD1 setae of A2 to A9, to A10, or to anal leg. More ventrad, horizontal dashes at lateral and subventral setae, or, on thorax, oblique dashes rising dorsad and caudad from SV1 setae, to L1 setae of following segments and L2

A
C. andromache
gray, markings black

B
C. andromache
med.gry; face white

C
C. benjamini
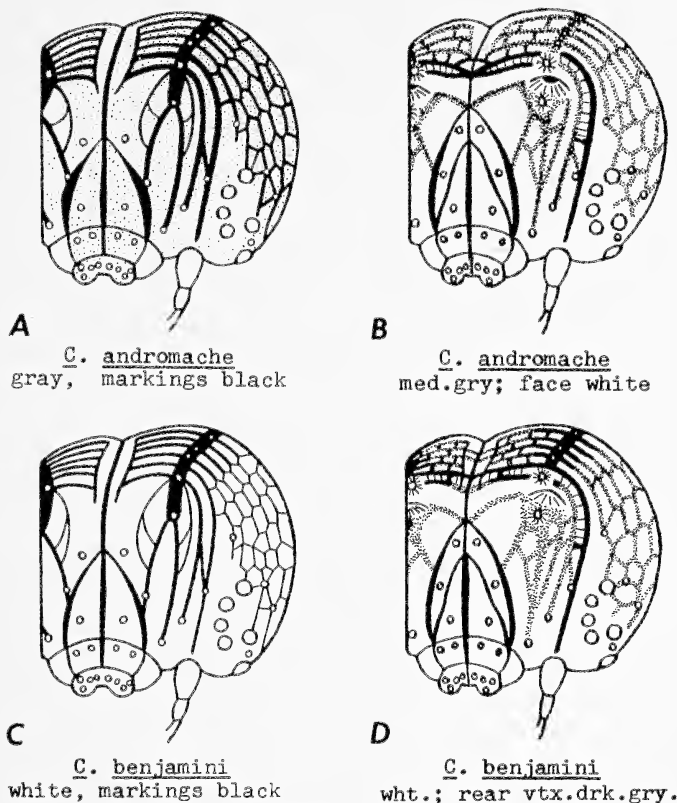white, markings black

D
C. benjamini
wht.; rear vtx.drk.gry.

Fig. 3. Schemata of the head patterns of: **A.** *Catocala andromache* second instar; **B.** same, fifth instar; **C.** *Catocala benjamini* second instar; **D.** same, fifth instar. Small circles, setal bases; large circles, ocelli. On fifth instar heads: stippled lines, gray; solid black, black; hatching between the lines of the facial rim, and rays around setal bases and prominence above seta P1, orange.

seta of A1. On sides of A1 to A6, to A8, or to A9, large patches enclosing spiracles, and sometimes adjacent setae. Leg tarsi white, brown or black; prolegs and anal legs often accented or striped. Venter pale, median spots brown or black, large on A1 to A4, reduced cephalad and caudad. The body tinted by ingested food after feeding.

The first instar larval traits of these six species of oak feeders agree with those of the first instar larvae of *C. ilia zoe* Behr, *aholibah* Stkr., *verrilliana beutenmulleri* B. & McC., *ophelia* Hy. Edw. and *delilah desdemona* Hy. Edw., all western oak feeders (Barnes and McDounough, 1913). The eleven species, in the first instar, have brown or black heads with black setae; bodies with long, black setae from prominent, dark bases, with three to five longitudinal, brown or black lines, and with dark patches on the sides of four or more abdominal segments.

Second instar larvae: (Figures 3A, 3C, 5A, 5C, 7A, 7C) Head colors in pale shades, setae black, or upper setae black, lower setae white. The head displays a pattern definitive for the six species, the pattern continuing into the final instar. Patterns black in the second instar, for all species other than *C. mcdunnoughi*. In *mcdunnoughi* the pattern is brown and incomplete, reaching full development in the final instar. Head pattern distinctive features are: black dorsal bars from P1 setae, through P2 setae, across vertex to the caudal margin. At sides of coronal suture, narrow lines diverging caudad. From these, sets of about six parallel lines cross the vertex and dorsal bars transversely, descending in parallel briefly, forming a genal reticulum below. In *C. chelidonia* and *mcdunnoughi* the lines remain sub-parallel to lower genae, and forward to ocelli. The two most anterior transverse lines descend anterior to ocelli, forming a double rim around front. Line 1, most anterior, descends to seta A2, sometimes forking, the lateral fork joining line 2 at seta A3. Line 2, more heavily marked, descends through seta A3 to antennal base. On the front, inverted Vs, their vertices at P1 setae, the mesal arms descending to, or near, setae AF1, the lateral arms descending to setae A1.

With one exception, body patterns resemble those of the first instar larvae. The three longitudinal lines may be supplemented with additional lines, to five or six. Spiracles yellow, with black rings, in all species. In most, segments A7, A8 and A9 have transverse dorsal ridges between the D2 setae, the setal bases enlarged and conical, ridge and setae largest on A8.

Fifth instar larvae: (Figures 3B, 3D, 5B, 5D, 7B, 7D) Features of fifth instar heads: face, perioral areas and mandibles white. Most pattern lines stippled in shades of gray, few lines in solid black. Dorsal bars from setae P2, narrow, sinuous, gray (but black in *C. benjamini*). Line 1, of frontal rim, gray or black dorsally, gray laterally. Line 2, gray in two species, heavily black in four. In these four, vivid orange fills between lines 1 and 2 dorsally and upper laterally. More posterior transverse lines on the vertex, narrow, sinuous, gray, interconnected. Genae reticulate in four species, in two species, parallel-lined below. In all species, pattern lines more interconnected, and detail variable between individual larvae in *C. chelidonia* and *C. californiensis*. Dorsal prominences orange in five species, with or without black centers (variable in *chelidonia* and *californiensis* larvae). Setae P1 and P2 gray to black, lower setae banded white, black, white. Body colors and patterns described under the species.

Species Descriptions

Catocala andromache Henry Edwards

Ovum: A female collected July 12, 1978, in Kern River Canyon, Kern County, California, gave two ova. Their mean diameter was 1.27 mm, the mean number of ribs, 64, at greatest diameter. The ova darkened two days before hatching on April 14 and 15, 1979.

First instar: Larval length at eclosion, 7 mm. Head and cervical sclerites dark brown, setae black. Body pale brown, markings very dark brown, becoming black later. Setae black, bases brown. On segments A1 to A4, a faint middorsal line. Along upper sides, three narrow, longitudinal lines. On lower sides, oblique dashes dorsad and caudad from thoracic SV1 setae; horizontal dashes through and below lower, lateral, abdominal setae. Large patches enclosing spiracles on A1 to A6.

Thoracic legs pale brown, tarsi black; abdominal legs pale brown. Venter whitish, median spots dark brown.

Second instar: (Figure 3A) Head medium gray, pattern lines in black. Upper setae black, lower setae white. Coronal and frontal sutures, and frons-clypeus midline narrowly black. Other characters as described under shared traits.

Body medium gray, with heavy dark gray and black pattern. Setae and bases black. Dorsum with dark gray midline bordered by straight, narrow, white dashes of equal length, these in turn bordered laterad, at the breaks, by similar dark gray dashes. Five dark gray and black longitudinal lines on the sides, the uppermost through dorsal setae from TI to A10 and anal valve. Ventrad four more lines through or between setae, all lines separated by pale gray; line 5 continuing on the anal leg. Dark gray lateral patches on A1 to A6. Segments A7, A8 and A9 with transverse dorsal ridges bearing the conical D2 setal bases, ridge and setae largest on A8. Thoracic legs black laterally, tarsi black; prolegs of A5 and A6 vertically striped. Venter pale gray, median spots black.

Third instar: Head as in second instar. Dorsal prominences evident above setae P1. Dorsal bar brown between setae P1 and P2, black from seta P2 caudad on vertex. Body without lateral patches. Segment A5 with a flattened black, middorsal tubercle, the center yellow. From tubercle, black stippling laterad, forming a patch on side between A5 and A6, to prolegs. Ventral filaments white.

Fourth instar: Much as in third instar. Head and body overall, dark gray.

Fifth instar: (Figures 3B and 4A) Head medium gray on vertex and genae, front white. Dorsal prominences orange, with black centers. P1 and P2 setae black, other setae white-and-black banded. Pattern lines mostly dark gray. Dorsal bars from setae P2 caudad, narrow, sinuous, gray. Transverse vertex lines narrow, gray, interconnected, the more caudal deleted near coronal suture. Genae reticulate. Line 1, of frontal rim, black dorsally, dark gray laterally. Line 2 heavy, black. Vivid orange between lines 1 and 2 dorsally and upper laterally. Coronal and adfrontal sutures black, frontal suture gray dorsad, black ventrad; frons-clypeus midline black.

Body color medium gray, with heavy dark gray and black stippling. Cervical sclerites dark gray, setae white-ringed. Dorsal and upper lateral setae black, dorsal setal bases orange, white-ringed; lower setae white. Middorsal line black, bordered by white; the white, bordered by gray; the gray, bordered laterally by a sinuous, heavy, black line, forming an undulating edge to the dorsum. A series of indistinct, interrupted, narrow longitudinal lines on the sides, separated by gray lenses. Tubercle of A5 short, black-stippled, center white with black dot. From tubercle, heavy black stippling laterad and ventrad between A5 and A6, to prolegs. On A7 to A9 transverse dorsal ridges with conical, orange D2 setal bases, ridges of A7 and A8 black-edged, black continuing ventrad and forward toward spiracles, ridge and setae largest on A8. Spiracles yellow. Thoracic legs black-lined, tarsi black. Prolegs and anal legs gray, setae white-ringed; anal legs black-stippled dorsally, heavily edged in black. Ventral filaments pink. Venter whitish, median spots dark brown.

Other data: Both larvae were identical in all instars. One adult male emerged June 13, 1979 (Figure 4B). The probable foodplants in Kern Canyon are: *Quercus wislizenii* Greene (Munz, 1974); on desert slopes, *Quercus turbinella californica* Tucker; on coastal slopes *Quercus wislizenii* and *Quercus dumosa* Nutt. The flight period begins about June 7 at 600 meters and after July 1 at 1500 meters. The species lives below the montane forest. It is known from San Diego County through

through the coastal ranges and the Sierras to Amador County, where the sub-
species *wellsi* Johnson (1983) replaces the lighter gray nominate *andromache* of
southern California.

Catocala benjamini Brower

Ova: Two ova were obtained from a female collected in 1977 by Erich Walter at
Pinyon Flat in the Santa Rosa Mountains, Riverside County, California. The
ovum mean diameter was 1.28 mm, the mean number of ribs, 53, at greatest
diameter. One ovum eclosed March 28, 1978.

First instar: (Figure 2) Larval length at eclosion, 6.5 mm. Head and cervical
sclerites dark brown, setae black. The body whitish, with pale gray dorsum the
setae black. On the sides, four longitudinal, dark brown lines, the uppermost
through the dorsal setae. Ventrad, three more lines, line 4 short, through the
abdominal L2 setae. All lines interrupted at A7, continuing on A8 and A9. Oblique
brown dashes rising dorsad and caudad from the thoracic SV1 setae. Horizontal
dashes subventrally on the abdomen. On segments A1 to A6, and on A8, large,
lateral, dark brown patches. Thoracic legs with black tarsi, abdominal legs pale.
Venter pale gray, median spots dark brown. Pattern lines, spots and patches
becoming black later.

Second instar: (Figure 3C) Head whitish, setae and bases black. Lines black,
genae reticulate. Coronal and frontal sutures and frons-clypeus midline nar-
rowly black.

Body white, setae and bases black, unlike first instar. Middorsal line pale gray
from TI to A9. At each side, and down the sides, broad, even, equal, frosty-white,
longitudinal stripes, separated by narrow, parallel, gray-stippled lines about two
dots wide, from TI to A10. No lateral patches on the abdomen. A8 and A9 with
transverse dorsal ridges with conical D2 setal bases. Thoracic tibiae and tarsi
black, prolegs whitish, anal legs black-striped. Venter white, median spots
black.

Third instar: Much as in second instar. Head nearly white, upper genae with
light brown patches, unlike the other species. The lines rimming the front, heavily
black. Upper setae black, lower setae white. A prominence above seta P1. Body
pale gray, setae and bases black. On A7 to A9 setal bases of D2 setae brown, coni-
cal. Middorsal line black-stippled, forming diamond-shaped patches on segments.
Body with alternating regular, longitudinal, equal stripes of white and less-white
body color, separated by narrow lines of black stippling. On A5 a small, flattened,
brown, middorsal tubercle. From tubercle laterad, black stippling, on sides form-
ing patches between A5 and A6, to the prolegs. Ventral filaments white.

Fourth instar: Much as in the third instar, progressing toward the fifth
instar pattern.

Fifth instar: (Figures 3D and 4C) Head pale gray, pattern in dark gray and
black. Setae P1 and P2 black, other setae banded. P1 and P2 setal bases orange-
ringed, head clear white around the setae. Dorsal prominences yellow orange, front
white. Vertex dark gray posteriorly; dorsal bars black from the P2 setae caudad.
The subparallel, transverse lines of the vertex narrow, interconnected, gray mesad,
black laterad across bar, gray ventrad, forming a genal reticulum. Line 1 of the
frontal rim gray, but black adjacent to dorsal bar. Line 2 black dorsally, gray
laterally. Vivid orange between the lines dorsally, absent in white area by seta P2,

again orange upper laterally. Coronal suture narrowly black, frontal and adfrontal sutures, and frons-clypeus midline, heavily black.

Body light gray, with undulating, indistinct, narrow, stippled black lines separating stripes of slightly lighter, and slightly darker body color. Middorsal line black. Dorsal and upper lateral setae black, lower setae white. All dorsal, subdorsal and upper lateral setae with raised orange bases. Segment A5 with a flattened, black-stippled, middorsal tubercle, the center gray. Laterally, between A5 and A6, gray and black stippling, forming patches on A6, with patches of light and dark brown stippling. Transverse dorsal ridges with large, orange D2 setal bases on A8 and A9, on A8 the ridge edge black-stippled, the stippling continued ventrad toward the spiracles. Spiracles yellow. Thoracic legs black-striped. Prolegs of A5 and A6 vertically gray-striped anteriorly, black-striped posteriorly; anal legs dorsally and laterally black-striped. Ventral filaments white; venter white, median spots black.

Other data: An adult male was reared from the ovum, emerging May 25, 1978 (Figure 4D). *Catocala benjamini* associates with the *Quercus turbinella californica* woodland on the desert slopes of the mountains from San Diego to Los Angeles
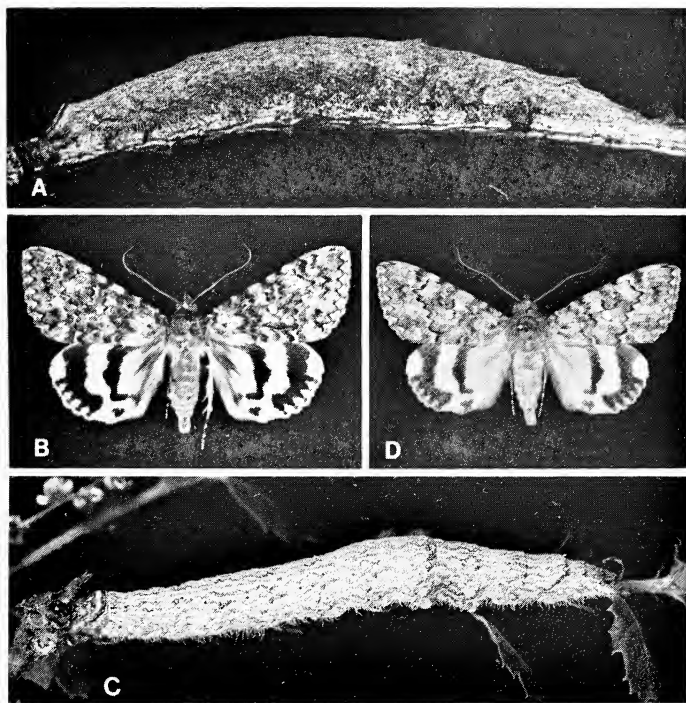

Fig. 4. **A.** *Catocala andromache* fifth instar larva, length 46 mm; **B.** the corresponding reared adult male, wing span 52 mm; **C.** *Catocala benjamini* fifth instar larva, length 42 mm; **D.** the corresponding reared adult male, wing span 48 mm.

Counties, and with *Quercus turbinella turbinella* Greene in the Providence and New York Mountains of the eastern Mohave Desert. At Pinyon Flat the flight period begins about June 1.

Catocala californiensis Brower

Ova: Females collected at Pinyon Flat, in the Santa Rosa Mountains, Riverside County, California, in 1978, yielded 46 ova. The ovum mean diameter was 1.16 mm, the mean number of ribs, 54, at greatest diameter. Three ova eclosed April 7,10 and 30, 1979. The first larva accepted the substitute foodplant, *Quercus dumosa*. The others did not feed, and died.

First instar: Length of the larva at eclosion, 5.5 mm. Head and cervical sclerites jet black, setae black. Body pale gray; dorsal and lateral setae and bases black, ventral setae white from black bases. A faint, discontinuous, middorsal dark line from TI to A10. On upper sides, three narrow, interrupted, longitudinal black lines, the uppermost through the dorsal setae. Large, black patches on A1 to A9, patches largest on A1 to A6. Horizontal, black dashes through thoracic and abdominal lower lateral setae and subventrally. Thoracic tibiae and tarsi black; prolegs and anal legs pale gray. Venter white, median spots black.

Second instar: (Figure 5A) Head medium gray, setae black. Genae reticulate, coronal and frontal sutures, and frons-clypeus midline, black.

Body whitish; setae and bases black, bases of the SD1 and L2 setae prominent on abdomen. Dorsum with a wide, pale-gray, middorsal stripe, divided by a narrow, white, interrupted midline. At the interruptions, short, narrow, white dashes at either side. On upper sides, three longitudinal dark gray lines, the uppermost heavy, through the dorsal setae, interrupted. On lower sides, horizontal dashes through setae and below. On A1 to A6, oval, dark gray patches. Between A5 and A6, dark gray stippling laterad from middorsal stripe, ventrad on sides to prolegs. Thoracic legs laterally black-accented, tibiae and tarsi black; prolegs flecked with black. Venter white, median spots black.

Third instar: Much as in second instar. Head pale gray, upper setae black, lower white. Bar between setae P1 and P2 deleted. A prominence dorsad of seta P1. No lateral abdominal patches. No middorsal tubercle on A5. Black stippling across dorsum of A5, on sides of A5 and A6 forming patches, reinforced by the longitudinal lines, to prolegs. Ventral filaments white.

Fourth instar: Progressing towards fifth instar. a middorsal tubercle on A5. Inconspicuous lateral gray patches on A1 to A6.

Fifth instar: (Figures 5B and 6A) Larva overall very white. Head: vertex pale gray, front and genae white. Lines of pattern medium gray. Dorsal bars from P2 setae sinuous, narrow, gray. The transverse, subparallel lines of vertex gray, interconnected, attenuated near coronal suture, laterad forming a reticulum on genae, becoming black ventrad. Line 1, of frontal rim, black at coronal suture, then gray, black near seta P2, gray laterad. Line 2 heavily black. Space between lines 1 and 2 orange dorsally and upper laterally. Setae P1 and P2 black, other setae banded. Bases of setae P1 and P2 orange-ringed. Dorsal prominences with orange patches, center black in two larvae, orange in one. Coronal and frontal sutures black, frons-clypeus midline black, becoming gray ventrad. Adfrontal sutures heavily black, an inverted black sagittate patch at apex of adfrontal sclerites.

Body white, dorsal setae black, others white. Bases of dorsal and subdorsal setae orange, other setal bases black. Dorsal setal bases prominent. Middorsal line

black, narrow, interrupted, from TI to A10, and to anal valve. To either side, a dorsal, longitudinal, sinuous black-stippled line mesad from dorsal setae. Next laterad, a longitudinal, interrupted, narrow black line tangent laterally to D1 setae, and through D2 setae. Ventrad, five more narrow, interrupted, longitudinal black lines. Between uppermost lateral line and line 2, and between lines 3 and 4, through spiracles, gray-stippled stripes, contrasting with white of body. Rising dorsad and caudad on sides of thorax and abdomen oblique, narrow, black lines passing through D2 setae, caudad of setae becoming heavy, black, short bars, convergent toward the dorsal midline on segments TII to A8. Middorsal tubercle of A5 flattened, white, with black stippling. From tubercle laterad, black stippling forming patches on sides of A5 and A6, to prolegs. an upwardly convex, strong, black crescent between spiracles on A5 and A6. On sides, from TII to A7, irregular darker patches, the patches intensified on abdomen as a bar between SD1 setae and L1 setae, crossing the spiracles obliquely. Segments A7 to A9 with transverse ridges bearing large, conical, orange D2 setal bases, ridges edged in black stippling; on A8, stippling continuing ventrad and cephalad to SD1 seta. Thoracic legs laterally black-accented, tarsi black. Prolegs of A3 and A4 with lateral, dark gray accents, prolegs of A5 and A6 vertically black-striped anteriorly and posteriorly, anal leg doubly black-striped. Spiracles yellow. Ventral filaments white. Venter white, median spots black.

Other Data: From the one ovum an adult male was reared (Figure 6B). It emerged June 8, 1979. A male and female *C. californiensis* were reared from two prepupal larvae collected at Pinyon Flat under shrubs of *Quercus turbinella californica* Tucker (Munz, 1974). *Catocala californiensis* is found on the desert slopes of the mountains from San Diego County to Los Angeles County, and in the woodland of *Quercus alvordiana* Eastw. in the Cuyama Valley, Ventura County. At Pinyon Flat the flight period begins about June 1.

Catocala johnsoniana Brower

Ova: Four ova were obtained from a female collected in 1978 in Kern River Canyon, Kern County, California. One ovum measured 1.29 mm in diameter, with 75 ribs at greatest diameter. The ribs were very narrow, and in low relief, making the egg smoother than those of other species. One ovum was fertile; it darkened two days before hatching on April 10, 1979.

First instar: The single first instar larva measured 6.5 mm at eclosion. Head and cervical sclerites jet black, setae black. Body medium gray, with heavy, black markings, making larva dark gray overall. Body setae and bases black. Dorsum medium gray with no midline. On uppersides three interrupted longitudinal lines, the uppermost tangent laterally to D1 setae, and through D2 setae, to A10. Line 2 above, and line 3 through, the subdorsal setae. On lower sides horizontal dashes at thoracic and abdominal setae. On sides of A1 to A6 large black patches, largest on A1 to A4. Thoracic tibiae and tarsi black, abdominal legs dark gray. Venter pale gray, median spots black.

Second instar: (Figure 5C) Head pale gray, heavily black-lined, appearing dark gray. Setae black. Genae reticulate; coronal suture, frontal suture, and frons-clypeus midline black.

Body pale gray, appearing dark gray because of heavily-black pattern; cervical sclerites black. Setae and bases black. On upper sides three longitudinal lines, the

uppermost, somewhat double, dark gray and black, through the dorsal setae. Second line dark gray, linked with line 1 at A7. Third line forming an interrupted series of oblique black dashes through SD1 setae, caudad and ventrad, to end at L1 setae of following segments, repeating to A6, and on A8 and A9. On lower sides interrupted, dark gray or black, horizontal dashes through and below setae. On A7, A8 and A9 transverse dorsal ridges bearing conical D2 setal bases. Thoracic tibiae and tarsi black, prolegs with black patches, anal legs laterally black-striped. Venter white, median spots black.

Third instar: Head as in second instar, pattern lines in dark gray and black. Black bars of vertex now from setae P2 caudad to rear margin. Setae P1 on dorsoventrally-elongated dark gray spots. Upper setae black, lower, white. Body much as in the second instar, overall dark gray. Upper setae black, lower white. Middorsal line strongly black. A series of about six indistinct longitudinal, generally parallel, black lines on sides. No middorsal tubercle on A5. Across dorsum of A5, and down sides between A5 and A6, dark gray shading, to prolegs. Dark gray lateral patches on A1 to A5. Ventral filaments sparse, short, white.

Fourth instar: Much as in third instar. From sides of thorax and abdomen a series of oblique narrow black lines rising dorsad and caudad through D2 setae, intensified caudad of setae on dorsum as short black bars, those of the two sides convergent toward middorsal line. On A5 a flattened, brownish gray, black-stippled, middorsal tubercle. No lateral patches.

Fifth instar: Larva dark gray overall (Figures 5D and 6C). Head vertex and upper genae medium gray, front and lower genae white. Setae P1 and P2 black. Other setae banded. Base of seta P1 black, of P2, orange-ringed. Prominence dorsad of seta P1 white, with orange patch and black center, patch tangent to P1 setal base. Dorsal bars sinuous, narrow, gray, from seta P2 to vertex rear margin. The sets of transverse lines on vertex, sinuous, interconnected, gray, the more posterior incomplete toward coronal suture, laterad passing into genal reticulum. Line 1, of the two lines rimming the face, black dorsally, gray laterally. Line 2, heavily black. Vivid orange filling between lines 1 and 2 dorsally and upper laterally. Coronal and frontal sutures narrowly black, frons-clypeus white with midline dark brown, bordered by gray dashes. Adfrontal sutures heavily black, adfrontal sclerites dark gray, with inverted sagittate, dark gray patch dorsad.

Body medium gray; cervical sclerites gray with setal bases white-ringed. Dorsal and upper lateral setae black, bases orange, D2 setae and bases largest; lower setae white. Middorsal line stippled, black; at either side light and dark gray stipplings. More laterad a dorsal longitudinal, sinuous black line through thoracic D1 setae, and mesad of abdominal dorsal setae to A10. On sides, four longitudinal, black lines, the uppermost through dorsal setae, the lines separated by gray stippling; fourth line through the L1 setae. Through spiracles, a longitudinal dark gray stripe between lines 3 and 4. On lower sides gray and black stipplings, darker above white ventral filaments. From sides of thorax and abdomen narrow oblique black lines rise dorsad and caudad through D2 setae, becoming short heavy dashes caudad of setae, those of the two sides convergent toward the dorsal midline. Middorsal tubercle on A5 pale brown, flattened, black-stippled, stippling continuing laterad and down sides of A5 and A6, reinforced at the longitudinal lines and stripes as patches, to prolegs. Segments A7 to A9 with transverse dorsal ridges between the enlarged, conical, orange D2 setal bases; ridge of A8 stippled in gray and black, stippling continuing laterad forward to SD1 seta. Thoracic legs dark gray, laterally

A

C. californiensis
white, markings black

B

C. californiensis
white; vtx.pale gry.

C

C. johnsoniana
gray, markings black

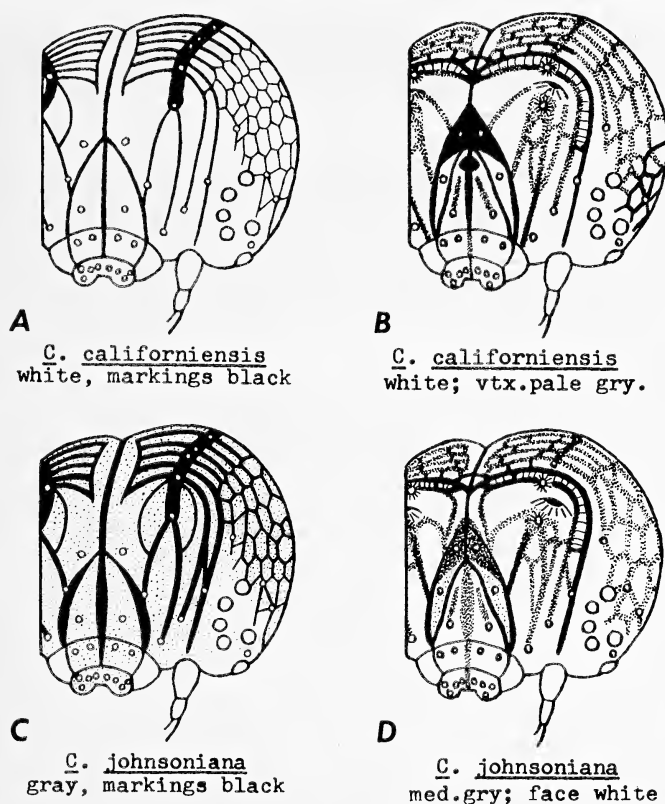**D**

C. johnsoniana
med.gry; face white

Fig. 5. Schemata of the head patterns of: **A.** *Catocala californiensis* second instar; **B.** same, fifth instar; **C.** *Catocala johnsoniana* second instar; **D.** same, fifth instar. Small circles, setal bases; large circles, ocelli. On fifth instar heads: stippled lines, gray; solid black, black; hatching between the lines of the facial rim, rays around setal bases and prominence above seta P1, orange. In *C. johnsoniana* the frons-clypeus midline is brown.

black-lined. Abdominal legs with dark gray patches and stipplings. Spiracles yellow. Venter white, median spots black.

Other data: An adult female was reared from the one ovum. it emerged June 9, 1979 (Figure 6D). *Catocala johnsoniana* has been collected at Hughes Lake, Los Angeles County; Kern Canyon, Kern County (several collectors); Coarse Gold, Madera County (Erich Walter); and Don Pedro Reservoir Recreation Area, Tuolumne County (J. R. Mori). It inhabits the Blue Oak woodland surrounding the California Central Valley. Besides the Blue Oak, *Quercus douglasii* H. and A., the woodland includes *Quercus lobata* Nee., and *Quercus wislizenii* A. DC. The foodplant is unknown. The flight period begins before that of *C. andromache* in the same area.
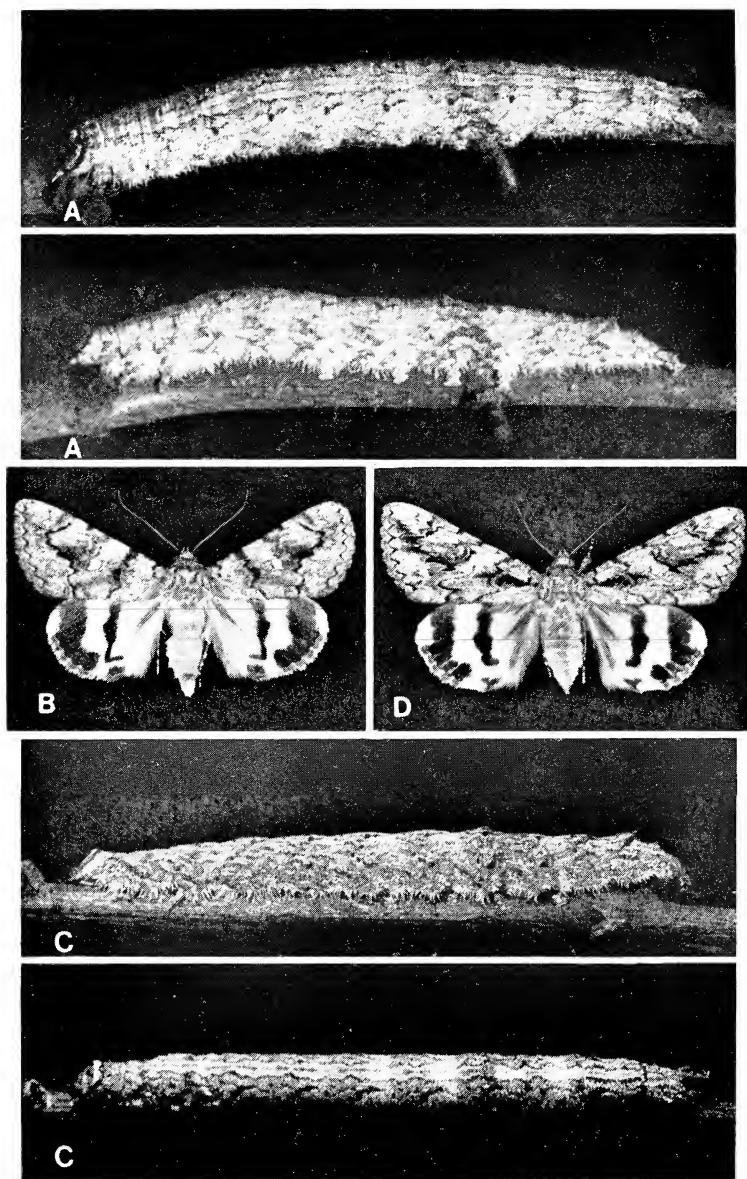
Fig. 6. **A.** *Catocala californiensis*, views of the fifth instar larva, length 37
mm; **B.** the corresponding reared adult male, wing span 46 mm; **C.**
Catocala johnsoniana, views of the fifth instar larva, length 44 mm; **D.**
the corresponding reared adult female, wingspan 50 mm.

Catocala chelidonia Grote

Only the fifth instar larvae of *C. chelidonia* were described by Crumb (1956). In 1978 and 1979 the author reared the species from ova to adults, and so the other stages may now be described.

Ova: Sixty-nine ova were obtained from 10 captive females collected at Pinyon Flat in the Santa Rosa Mountains, Riverside County, California, in 1977 and 1978. Of these, 42 were fertile, hatching from April 11 to May 22. Of the larvae, 15 pupated, producing 11 adults. The ovum mean diameter measured 1.02 mm, with a mean of 64 ribs at greatest diameter.

First instar: The larvae measured 5 mm at eclosion. Head and cervical sclerites dark brown, setae black. Body whitish, setae black, bases brown. A wide longitudinal, unmarked stripe on dorsum between the lines through dorsal setae. On upper sides three longitudinal, black lines, line 2 most continuous; line 3 continuous on thorax, on abdomen forming a series of oblique dashes through SD1 setae, caudad and ventrad, ending on L1 setae of following segments, repeating to A9, absent on A7. Large, lateral, black patches on A1 to A5, smaller on A6 and A8. Thoracic legs white. Prolegs of A5 and A6 vertically striped in dark brown; anal legs brown-striped laterally. Anal valve brown. Venter white, median spots dark brown. Body markings darkening to black later.

Second instar: (Figure 7A) Head pale gray, upper setae black, lower white. Pattern lines black. Across vertex and ventrad on genae, a set of parallel lines, little interrupted, unlike the reticulate genae of four species. Coronal, frontal sutures, frons-clypeus midline, black.

Body pale gray, setae and bases black, setal bases prominent. The pattern much as in first instar. Dorsum more gray than sides; a middorsal line from TI to anal valve, paralleled by narrow, dorsal, discontinuous, dark gray lines through thoracic D1 setae and mesad from abdominal dorsal setae to A8. On upper sides, three longitudinal, interrupted, black lines, the uppermost through dorsal setae, the most ventrad forming a series of oblique dashes through SD1 setae. Short, oblique, black dashes rising caudad from thoracic SV1 setae. On abdomen, horizontal dashes through lower setae. Large, black patches on A1 to A6, and A8. On A7 to A9, transverse dorsal ridges between the conical D2 setal bases. Thoracic legs black accented, tarsi gray. Prolegs of A5 and A6 gray. Anal legs with heavy, black dorsal stripes, laterally doubly black-lined. Venter white, median spots black.

Third Instar: Head white, lines black, like second instar. White prominences dorsad of setae P1. Genae reticulate above, parallel-lined below. Body pale gray, or gray cephalad and brown caudad, or entirely pale brown. Brown phases appearing in larvae confined in dim light. Middorsal line black. Laterad and down sides, six interrupted, longitudinal, black, or, on brown larvae, dark brown, lines; the first line on dorsum mesad from dorsal setae. Between lines 1 and 2 through dorsal setae, the body darker, making a dorsal, longitudinal, dark stripe to either side of the pale gray middorsal area and black midline. A5 with black-stippled tubercle, the center pale gray. From tubercle laterad, black stippling on sides, forming gray and black patches in gray larvae, and orange and brown patches in brown larvae, to prolegs. Single, white, ventral filaments on A1 to A5.

Fourth instar: Much as in third instar. Ventral filaments numerous.

Fifth instar: (Figures 7B and 8A) Head whitish, setae P1 and P2 black, others banded. Prominences dorsad and laterad of setae P1, orange, with or without black

center. An orange bar between setae P1 and P2, P1 base black, P2 base orange, ringed by yellow, the head pale yellow around setae. Dorsal bar narrow, sinuous, gray from seta P2 caudad to vertex rear margin. Transverse lines of vertex gray, interconnected, reduced near coronal suture, laterad anastomosing on upper genae, joining parallel lines ventrad, forward to ocelli. Frontal pattern like the other species. Pair of lines rimming front gray dorsally, black adjacent to seta P2, gray, or gray and black laterally. No orange between lines. Adfrontal sclerites white, adfrontal sutures heavily dark gray, to black. Coronal, frontal sutures, narrowly dark gray, to black. Frons-clypeus mesally white, laterally gray, midline black.

Body, whitish, or pale brown, lines gray and black, or brown. Cervical sclerites gray, setal bases orange, white-ringed. Dorsal and upper lateral setae black, bases orange; lower setae white, bases black on thorax, yellow on abdomen. Middorsal line black, bordered by pale gray or pale brown stripes. Three longitudinal lines in black, or brown, on the upper sides from TI to A9, or A10, the uppermost through dorsal setae interrupted. Line 2 black or dark brown, bordered by gray and black, or brown, forming a longitudinal stripe to A10. Line 3 gray and black, or brown, interrupted. Longitudinal dashes in gray and black, or brown on the sides. On A5, a short erect, black stippled middorsal tubercle, center orange-brown to pale brown, the tubercle on a transverse black-stippled ridge, stippling continuing ventrad on the sides of A5 and A6, forming interrupted, oblique patches, becoming brown, to prolegs. Tubercle and lateral patches on A5 and A6, most prominent of six species. On A8 and A9 prominent transverse dorsal ridges between large, conical D2 setal bases. Ridge of A8 margined in orange-brown, black-stippled, stippling continued ventrad forward to SD1 seta. Thoracic leg tibiae black-lined, tarsi black. Prolegs of A3 and A4 pale gray, or brown, with dark accents; prolegs of A5 and A6 laterally mottled in dark shades. Anal legs stippled darkly dorsally, and laterally striped in dark gray. Setal bases of thoracic and abdominal legs white-ringed. Spiracles yellow. Ventral filaments white; venter whitish, or pale brown, median spots very dark brown, edged in vivid dark red.

Other data: From the first ovum an adult female was reared. It emerged June 9, 1978. Ten adults were obtained in 1979 (Figure 8B). In California, *C. chelidonia* is known from the desert slopes of the mountains of San Diego and Riverside Counties where it inhabits the *Quercus turbinella californica* woodland that includes *Agave deserti* Engelm., the agave being a reported nectar plant for *C. chelidonia* (Barnes and McDunnough, 1918, p. 33).

Comparison of Arizona and California C. chelidonia Larvae

Crumb's (1956) *chelidonia* larvae were from Arizona. The larvae from California differ in a number of traits.

Arizona *chelidonia* larvae range in color from pale gray to blackish; the California larvae that were reared were pale gray or pale brown. The heads of Arizona larvae have white or orange prominences, California larvae show orange prominences. The most dorsal large setae from black spots in Arizona larvae, and from orange and yellow rings in California larvae. Arizona larval heads have double black lines rimming the face; those of California, double gray lines. The occiputs (vertices) of Arizona larvae are reticulate; those of California larvae are subparallel lined. No frontal inverted Vs are described for Arizona larvae, but are prominent head

features in California larvae. The genae of California larvae are parallel-lined below (no data for Arizona larvae). The thorax in Arizona larvae has a dark shade dorsally on TII, no shade present in California larvae. In Arizona larvae the A5 middorsal tubercle is long, drooping posteriorly; the tubercle is short, and erect in California larvae. The spiracles of Arizona larvae are brown, of California larvae, yellow. The venter of Arizona larvae is blue, with purple median spots. California larvae have white or pale brown venters, with dark brown median spots edged in vivid dark red.

Catocala mcdunnoughi Brower

Ova: One ovum was yielded by a female collected in Potato Canyon in the San Bernardino Mountains, San Bernardino County, California, in 1978. The diameter measured 1.27 mm; the ribs numbered 61 at greatest diameter. The ovum changed from yellow to golden brown two days before hatching on May 14, 1979.

First instar: The length at the first feeding, 7 mm. Head and cervical sclerites, golden brown, setae black. Body pale yellow, lines of the pattern in bright brown. Setae and bases black. Dorsum yellow, forming a wide longitudinal stripe between the lines through dorsal setae, as in *chelidonia*. On dorsum a faint, narrow, brown midline. On upper sides, three longitudinal lines, the uppermost through dorsal setae, interrupted; line 2 more continuous, to A10 and down anal leg. Line 3 forming a series of oblique dashes through SD1 setae, caudad and ventrad, ending on L1 setae of following segments, repeating to A9, absent on A7. On lower sides horizontal dashes through L2 setae and subventrally, lowest continuing as a broad stripe on anal leg. On A1 to A5 large lateral brown patches, A6 patch smaller. Thoracic legs white, tarsi brown; prolegs, with lateral, dark-brown patches; anal legs with brown patches and stripes. Venter pale yellow, median spots dark brown. Larva golden brown overall, like the golden brown young shoots of *Quercus chrysolepis* Liebm.

Second instar: (Figure 7C) Head pale yellow, pattern brown. Vertex yellow, unmarked. From its lateral edges arise anastamosing dark brown lines, of these, two form a lateral rim on front. Other lines descend subparallel on genae, forward to ocelli. No vertex bars from P1 and P2 setae to caudal margin. The frontal pattern with inverted Vs incomplete dorsally. Coronal, frontal sutures, frons-clypeus midline, dark brown.

Body pale golden yellow, pattern in brown. Cervical sclerites pale yellow, brown-edged. Setae and bases, black. Middorsal line brown. To either side a dorsal, longitudinal line through thoracic D1 setae and mesad from abdominal dorsal setae. On sides, five longitudinal lines, the uppermost through dorsal setae. Lines 4 and 5, interrupted. More ventrad, a final series of horizontal dashes through the L3 setae. On A1 to A5, brown lateral patches. On A8 and A9 transverse dorsal ridges between the prominent D2 setal bases. Thoracic legs yellow, tarsi brown. Prolegs and anal legs yellow. Prolegs brown-accented, anal legs striped. Venter pale yellow, median spots dark brown.

Third instar: Head white, pattern lines dark brown, much as in second instar, caudal margin black. On vertex, narrow brown loops along brown coronal suture. Orange bar between setae P1 and P2. On genae, parallel brownish-black lines. On front, complete inverted Vs. Upper setae black, lower setae white. Body similar to the second instar, lateral patches now pale gray, indistinct. No middorsal tubercle

on A5. D2 setal bases on A8 black, ringed in orange-brown; on A9, ringed in brown. No ventral filaments.

Fourth instar: Lines of the head in gray and black. Vertex crossed by six transverse subparallel lines from irregular lines by coronal suture; the transverse lines faint caudad of P2 setae, laterad forming a reticulum on upper genae, joining parallel lines below. Front rimmed by a gray and a black line, frontal pattern gray. Body similar to third instar. Ventral filaments white, short, sparse; no lateral patches. No A5 middorsal tubercle.

Fifth instar: (Figures 7D and 8C) Head white with yellow and black caudal margin. Setae P2 and L1 dark gray, P1 light gray, others white. P1 and P2 setal bases ringed by orange, orange continuous from P1 to orange prominence dorsad from P1. Vertex transverse lines gray, subparallel, interconnected, arising from an

A

C. chelidonia
white, markings black

B

C. chelidonia
white; vtx.pale gry.

C

C. mcdunnoughi
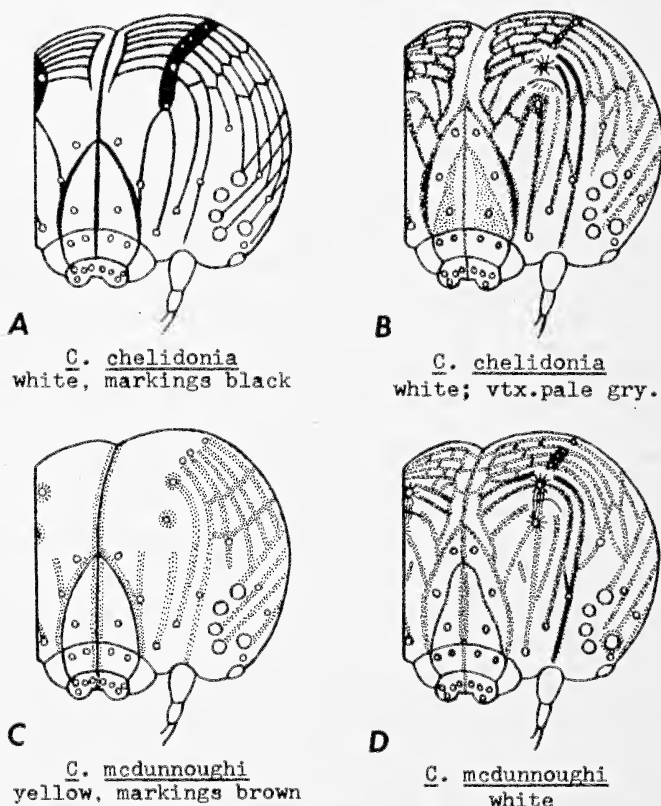yellow, markings brown

D

C. mcdunnoughi
white

Fig. 7. Schemata of the head patterns of: **A.** *Catocala chelidonia* second instar; **B.** same, fifth instar; **C.** *Catocala mcdunnoughi* second instar; **D.** same, fifth instar. Small circles, setal bases; large circles, ocelli. On fifth instar heads: stippled lines, gray; solid black, black; hatching between the lines of the facial rim, rays around setal bases and prominence above seta P1, orange.

irregular line by coronal suture. Upper genae, reticulate; below, the lines sub-parallel, forward to ocelli. Short gray bars on the vertex between setae V1 and V2. Lines rimming front gray dorsally and laterally, no orange color between them. The coronal, adfrontal, and frontal sutures gray, frontal suture arms nearly black ventrad. Frons-clypeus midline gray.

Body nearly white; cervical sclerites gray, their setal bases white-ringed. Upper body setae dark gray, lower, white. Dorsal and lateral setal bases orange, prominent, on TII to A9. On TI and A10 the setal bases black, less prominent. Middorsal line gray and black. To either side, and on sides, seven indistinct, narrow, longitudinal, gray and black lines. Between lines, longitudinal, stippled lineations; all lines subdued, larva appearing white. Segment A5 swollen, tubercle replaced by a smooth transverse swelling. Narrow, black stippling on the intersegmental membrane between A5 and A6. A8 transverse dorsal ridge prominent, meeting a longitudinal raised fold middorsally, forming a T. A8 D2 setal bases orange, conical. Ridge and setae lesser on A9. Thoracic legs with lateral brown patches, leg setae from white basal rings. Prolegs and anal legs pale gray, the setae from white basal rings. Prolegs narrowly, vertically, brown striped; anal legs brown-stippled and with narrow, brown, lateral lines. Spiracles yellow. Ventral filaments white. Venter white, median spots brown. The smooth white larva, with node-like head and
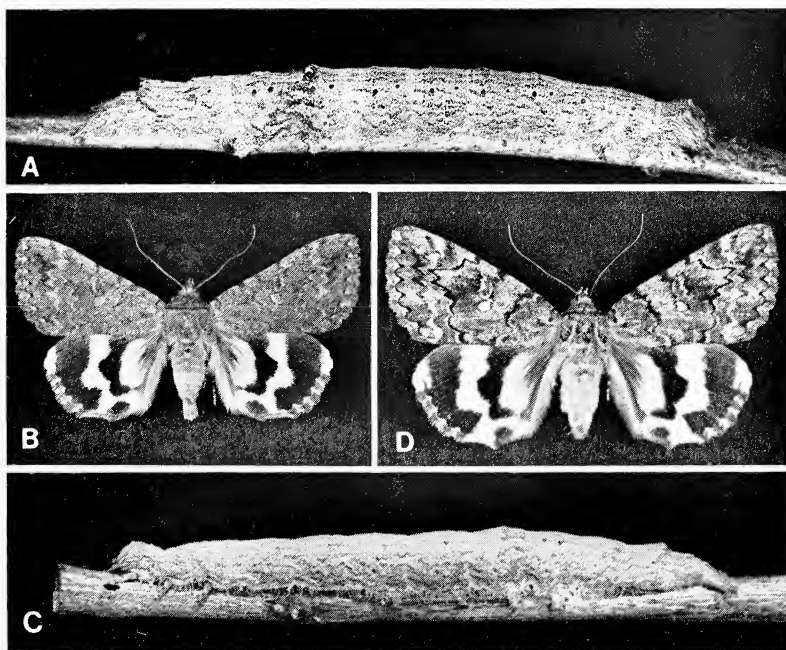

Fig. 8. **A.** *Catocala chelidonia* fifth instar gray larva, length 37 mm; **B.** same, adult male from a gray larva, wing span 48 mm; **C.** *Catocala mcdunnoughi* fifth instar larva, length 52 mm; **D.** same, adult female from the larva, wing span 52 mm.

small prothorax, blends well with the smooth, white branchlets of *Quercus chrysolepis*.

Other data: From the one ovum a female was reared, the moth emerging July 2, 1979 (Figure 8D). The species is found in the montane forest from San Diego County northward to the northern Sierra Nevada Range in Amador County, where the subspecies *browerarum* Johnson (1983) with green-scaled, very dark brown wings replaces the typical, medium-brown populations of southern California. The foodplant surely is *Quercus chrysolepis*, to which the larval coloration is perfectly adapted, and which, in some habitats, is the only oak available for the *C. mcdunnoughi* populations that exist there. The flight period, in southern California, begins after July 15; in central California, from June 20, onward.

Discussion

1. Rearing Observations

Females of the six species were confined in large paper bags and two-liter cardboard cylinders with open, net-covered ends. They were fed nightly with sugar water in cotton and with watermelon slices. Open windows maintained normal temperature and humidity ranges in the room. Each container held a sprig of foodplant stapled to a corrugated cardboard square wrapped loosely in netting. Ova were found in the netting, in holes of the cardboard edges, on container surfaces, in seams and corners, but never on foliage. Oviposition success was about the same in both container types. Moths lived from two to thirty-six days in captivity.

Captive females yielded ova infrequently. The percentage of fertile ova was low. As the captive females died, they were dissected to determine if their ova were exhausted. In 69 dissections, only one female was found without ova. It had laid one egg, the last, that proved to be fertile. Most females held numerous, fully-formed ova, with additional undeveloped ova. As many as 101 developed unlaid ova per female were counted. It seems evident, that the reproductive potential of these small moths exceeds 100 ova per female.

To retard the eclosion of the ova before the opening of the buds of the foodplants, the ova were held outside most of of the winter, and for the month of January put in refrigeration at about 5°C. Eclosion occurred at about the dates when oak buds open in nature.

1. The larvae were reared on foodplants held in glass cylinders with netting at the open ends. This permitted observation of the larvae at all times. In 1979 the 41 *C. chelidonia* larvae, when confined together, caused each other to drop from the foodplant. A number of larvae perished before regaining the foodplant. A change to confinement in small containers resulted in more losses to disease, perhaps the result of high humidities from the confined foliage. The surviving larvae were spread out in cylinders and wooden rearing boxes. Fourteen larvae reached pupation, producing ten adults. In the boxes, under low light

intensities, some of the *chelidonia* larvae at the third and later instars changed from gray to mottled gray and brown, or to brown coloration. None of the larvae in the well-lit cylinders changed color, remaining gray. Leaf litter was provided for pupation. All larvae pupated in the litter but one. The *C. johnsoniana* larva spun a tight cocoon well above the litter in the foodplant foliage.

Larval growth was rapid. The mean durations of the instars for five of the species were: first instar, five days; the second, four; the third, four; the fourth, four; the fifth instar to spinning, eight days. The mean length of the total larval period was 24.5 days. The pupal period from spining to emergence averaged 35.7 days. For these species, larval development in nature may be about as rapid, as the reared adults emerged within the natural flight periods. The larva of *C. mcdunnoughi,* a high mountain species, in the coastal environment with mild nights, grew very rapidly, emerging as an adult well before the flight period in the mountains. Five species were reared on *Quercus dumosa. C. mcdunnoughi* was reared on *Quercus chrysolepis.*

Feeding behavior: First instar larvae fed both by day and night. Between feedings they rested beneath leaf edges, on veins, or on midribs. At rest the larvae attached themselves by the abdominal legs, the body forward of A5 being raised at a slight angle. The thorax and head were bent again parallel to the surface, with the thoracic legs appressed forward against the thorax, and the head extended, the front uppermost. In this attitude, and colored by consumed food, the larvae resembled closely the stipules of opening oak shoots. In the second instar feeding was done chiefly at night, the larvae resting, head downward, on leaf petioles and twigs between feedings. In older instars all feeding was done at night, the larvae resting by day on twigs, usually head downward. After periods of activity, in all instars, a pulsation between segments A8 and A9, in the form of a pinching-in of the sides, was observed at times.

2. Constancy of Larval Traits

While the number of larvae available for comparison was small, the larvae shared many traits, as well as exhibiting species differences in color and pattern details. The author has observed, in other species of California *Catocala*, that variations between larvae of a species in the first and second instars is minimal. The larval size, color and patterns are constant, and the larvae alike. It is believed that the species similarities and differences exhibited by the small sample of larvae in the first and second instars will be found to be valid when additional larvae are seen. Likewise, head patterns have much constancy in the second and later instars, even when variations are extensive in the body colors of the larvae of a species. The observed similarities and differences in head patterns should prove to be valid also.

Traits shared between the species in the first two instars, and in the head patterns from the second to final instars, indicate that the six species are closely allied. In the future, comparative studies of pupae, of adult wing patterns and forms (Johnson and Walter, 1980), of the male genitalia and of the internal and external female genitalia should afford further insights into the interrelationships of the six species.

3. Larval Keys

a. FIRST INSTAR LARVAE

1a. Body* pale yellow, all markings in bright brown, head golden brown...*C. mcdunnoughi*

1b. Body white, pale brown, or gray, markings dark brown to black, heads dark brown to black.....................................2

2a. Body, overall, obviously dark in color 3

2b. Body, overall, pale gray to whitish....................................4

3a. Body ground color medium gray, no middorsal line, head shining jet black, dashes on the lower sides of the thorax and abdomen horizontal, all body markings and setal bases black from eclosion ....*C. johnsoniana*

3b. Body ground color pale brown, head dark brown, a short middorsal line on A1-A4, dashes on the lower sides of thorax oblique, of abdomen horizontal, markings and setal bases brown at eclosion, becoming black later................*C. andromache*

4a. Six black lateral patches, longitudinal line 3 on the abdomen interrupted as a series of oblique dashes through the SD1 setae to end on the L1 setae of following segments, repeating; head dark brown, body white, markings brown and black, becoming all black later.................................*C. chelidonia*

4b. Seven or nine lateral patches, longitudinal line 3 horizontal, not a series of oblique dashes..5

5a. Seven lateral patches, four longitudinal lines on sides of the body, head dark brown, lines and setal bases black, ventral spots dark brown, darkening to black later.....*C. benjamini*

5b. Nine lateral patches, three longitudinal lines on the sides of the body, head shining jet black, all body markings jet black at eclosion...*C. californiensis.*

*All larval bodies became tinted by food in the gut; greenish in five species, golden brown in *C. mcdunnoughi*.

b. SECOND INSTAR LARVAE

In the second instar the definitive head patterns appear, while, in five species, the body traits of the first instar are retained. In *C. benjamini* all traces of the first instar pattern disappear. In *C. chelidonia* and *C. mcdunnoughi*, which share a wide dorsal stripe in the first instar, the

lower genae are parallel-lined, and longitudinal line 3, of the body, forms a series of oblique dashes through the SD1 setae to the L1 setae of the following segments. Reticulate genal patterns are found in the other four species. The separation of the six species into a group of two, and a group of four, is reinforced by additional differences in later instars.

1a. Head and body ground color pale yellow, markings bright brown; genal pattern definitely parallel-lined below; head vertex unmarked, inverted Vs of the front incomplete; body setae and bases black; six lateral longitudinal lines; body lines, five lateral patches, and ventral spots all brown........ ....*C. mcdunnoughi*

1b. Head and body color white to gray, head markings black, body markings mostly gray or black..................................2

2a. Genae entirely reticulate. On the body, the uppermost longitudinal line through the thorax D2 setae and the abdominal D1 and D2 setae; six lateral patches, or none...................3

2b. Genae markedly parallel-lined; on the body, the uppermost longitudinal line through the thorax D1 setae, and mesad from the abdominal D1 and D2 setae; seven lateral dark gray patches; head and body pale gray, dorsum darker than the sides, body contrastingly striped in gray and black ....*C. chelidonia*

3a. Lateral patches lacking; body evenly, longitudinally, striped in white, the stripes parallel, separated by very narrow, dark, gray-stippled lines; middorsal line pale gray, setae and bases black, ventral spots black.............................*C. benjamini*

3b. Lateral patches present, body pattern much as in the first instar 4

4a. Heads and bodies, overall, obviously dark gray 5

4b. Head and body very pale gray, the body dorsum with a pale, longitudinal stripe with gray midline, the line regularly interrupted; at either side, narrow, interrupted gray lines, the segments alternating with those of the middorsal line; three lateral, longitudinal, dark gray lines, the first through the dorsal setae, the third continuous through the SD1 setae; gray lateral patches on A1 to A6........................*C. californiensis*

5a. Five dark gray to black, heavy, lateral, longitudinal lines, the uppermost through the dorsal setae, line 3 continuous; head and body appearing dark gray overall from heavy markings; dark gray middorsal line bordered by narrow, broken, white lines, these laterally by narrow, broken, gray lines, the breaks of the two series alternating; dark gray lateral patches on A1 to A6..*C. andromache*

5b. Three dark gray to black, heavy, longitudinal, upper lateral

lines, the first through the dorsal setae, line 3 an interrupted series of oblique dashes through the SD1 setae to the L1 setae of the following segments; head and body appearing dark gray from heavy pattern; gray middorsal line without bordering alternating gray and white dashes; dark gray lateral patches on A1 to A6 ....*C. johnsoniana*

c. FIFTH INSTAR LARVAE

In the fifth instar differentiation between the species reaches a maximum. The lower genae of *C. chelidonia* and *C. mcdunnoughi* retain a pattern of straight lines. In both, the pair of lines rimming the face are gray and free of orange coloring. In the third and fourth instars the ventral filaments develop tardily in both. The larvae confirm an alliance between the two species first observed by Brower (1937) in a study of their adult characters.

Of the four species with reticulate genae, all display a black facial rim with orange coloring between the two lines rimming the face. Two of the four, *C. californiensis* and *C. johnsoniana*, in the fourth and fifth instars develop a series of jet black bars on the dorsum caudad from the D2 setae, forming a distinctive convergent pattern, unlike *C. andromache* and *C. benjamini*. At the apex of the adfrontals is a sagittate patch in *californiensis* and *johnsoniana*. In the first instar their larvae, only, eclosed with shining, jet black heads, and jet black body markings. The A5 middorsal tubercle appears in the fourth instar. These characters, taken with adult wing characters that set them apart from *andromache* and *benjamini*, suggest a greater degree of alliance between them than with the other two species.

The interrelationships of *C. andromache* and *C. benjamini* await further knowledge. Three disjunct populations of *C. benjamini* exist, those of the desert slopes of the California coast ranges; a population in the eastern Mohave Desert in the Providence and New York Mountains; and the Arizona population from which *benjamini* was first described. The immature stages of the Pinyon Flat population are the only stages of the species presently known. These differ markedly from *C. andromache*. The *benjamini* adults from Pinyon Flat also differ markedly, both from *andromache*, and from Arizona *benjamini*. Comparative studies of the adults of the three *benjamini* populations, and of *andromache* are required, together with comparative studies of the larvae of all of these entities; additional examples of larvae of *andromache* and Pinyon Flat *benjamini* are needed as well.

The keys to the first and second instar larvae, whose characters are more stable, will probably stand as is. The construction of keys for *Catocala* larvae of later instars when based upon small samples of larvae offers more difficulties due to the greater variability in color that the larvae

of some species display. In constructing a key to the fifth instar larvae, the author has relied chiefly on traits that tend to remain constant during variation in color. This may make the key more serviceable.

The key has been prepared to fit into Crumb's key, it being necessary to modify two of his statements in order to incorporate into it the six species of this study. My key includes, from Crumb's key, only the statements that lead to the separation of the six species. Other statements must be followed in his key. Crumb's number sequences have been used, with letters *a* and *b* added, to clarify which of a pair of Crumb's choices is being used. The two modified statements are starred with asterisks, and the changed wording underlined. To accomodate the additional six taxa, Crumb's number sequence has been extended.

1a. With a middorsal hump, horn, or transverse ridge on abdominal segment 5. A fringe of fleshy filaments present laterally on the venter. Mandible with a free basal process bearing on an apical molar area (pl. 11, *C*.). Head often distinctly protuberant between setae P^1 and P^2 20

20b. 37

*37b. Skin without granules. Setigerous tubercle II at least somewhat elevated throughout on abdominal segments. Spiracles brown, *or yellow* 38

38b. Middorsal prominence on abdominal segment 5 a transverse, low, rounded hump, usually with a short subconical projection medially and without a secondary horn or other prominence 39

39a. Feed on oak 40

*40b. Head usually distinctly protuberant between setae P1 and P2, *the face often with inverted black Vs with vertices at setae P1, and rimmed by a double line anterior to the ocelli, giving the front a strongly lined appearance*, sides and tops of head not reticulate with red, *Arizona and California* species 47

47a. The two lines rimming the face anterior to the ocelli lacking an orange color filling the space across the vertex and dorsad of ocellus I 48

47b. The two lines rimming the face anterior to the ocelli with orange color between the lines on the vertex and laterally dorsad of ocellus I 50

48a. Larvae with brown spiracles, body pale gray to blackish; lines of vertex and genae of head tending to be reticulate; the fifth abdominal segment median dorsal tubercle long, drooping posteriorly; larval ventral surface blue, median spots purple; thorax II with dark, dorsal patch...........Arizona *chelidonia*

48b. Larvae with yellow spiracles, the body white to pale brown;

lines of the vertex and lower genae tending to be parallel; the fifth abdominal segment median dorsal tubercle short, erect, or reduced to a transverse swollen ridge; venter nearly, or quite white, or pale brown, median spots brown; no dorsal dark patch on thorax II 49

49a. Larva nearly white, lineations much subdued; median tubercle of abdominal segment 5 reduced to a smooth transverse fold, the segment swollen; the venter white, median spots brown ....*mcdunnoughi*

49b. Larva pale gray to pale brown, prominently lined in dark gray, or black, or brown; median dorsal tubercle of abdominal segment 5 short, erect; venter whitish or pale brown, median spots dark brown edged in red ....California *chelidonia*

50a. Larvae with dark gray or black sagittate patch on the adfrontals; the dorsum of the body with a series of jet black bars or ashes convergent from the D2 setae towards the midline..........51

50b. Larvae lacking an inverted sagittate patch on the adrontals; the body dorsum lacking a pattern of black bars or dashes convergent from the D2 setae..52

51a. Head with black sagittate patch on the adfrontals; the larva almost white, a middorsal black line on a median, wider, dorsal, longitudinal, white stripe edged by a dark gray line laterally. Lateral longitudinal, gray and black lineations reduced; dark patches on the sides across the spiracles from TI to A9, most prominent on A1 to A3...........*californiensis*

51b. Larva with a gray sagittate patch on the adfrontals; the larva very dark gray, with complex pattern of contrasting light and dark gray, or black, patches and lineations......*johnsoniana*

52a. Head pale gray, face white, rear vertex dark gray, a black bar caudad of seta P2, orange rim absent from white area around seta P2; larva nearly white, the narrow, numerous, longitudinal gray lineations subdued; median tubercle of abdominal segment 5 on a prominent transverse ridge..............*benjamini*

52b. Head medium gray with heavy markings, appearing dark gray; the bar from the P2 seta caudad on the vertex narrow, sinuous, gray, the facial rim with continuous orange coloring; the larva very dark gray, the longitudinal lineations indistinct in general, heavy, gray and black stippling..........*andromache*

statement reworded in part

to Mr. Ralph E. Wells for specimens and assistance on species distribution; to Mr. James R. Mori for like assistance and the use of his mountain home; to Mr. Larry Shaw for *Catocala* specimens; to Mr. and Mrs. Erich Walter for sharing in these studies; to Dr. Charles L. Hogue and Mr. Julian Donahue of the Los Angeles Museum for reference assistance; and to my wife Ruth for steadfast support and participation in the field work.

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Announcement

The *Journal of Research on the Lepidoptera* and the *Journal of the Lepidopterists' Society* are the sole contact with the literature on butterflies for a significant portion of the readership of those publications. The editor of this journal, acknowledging the value of alerting all lepidopterists, not just professional biologists, to work on the biology of butterflies, has proposed a regular bibliographic series citing recent, top quality works on the ecology, genetics, and evolutionary biology of butterflies. The just published proceedings of the Symposium on the Biology of Butterflies (held at the British Museum of Natural History in South Kensington, London) has an extensive bibliography of work preceding the autumn of 1981. This survey, therefore, will commence with 1982 in this volume of the *Journal of Research on the Lepidoptera*. 1983 and 1984 along with the start of current citations will be in volume 24.

Although I have agreed to initiate this regular offering, I acknowledge both my limitations and the biases inherent in solo authorship. I would like to request assistance in this pursuit. Please let me know of your recent and upcoming published works, particularly if these will appear in relatively obscure, irregularly published or hard-to-find foreign journals.

Dennis D. Murphy, Dept. of Biological Sciences, Stanford University, Stanford, California 94305

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Notes

A Homoeotic *Agraulis vanillae incarnata* (Nymphalidae)

A male homoeotic *Agraulis vanillae incarnata* (Riley) was collected 27 October 1963 at Ventura College, Ventura, California. The undersides of the forewings display the condition (Figs. 1 and 2). On the left forewing, the homoeotic patterns consist of a ring of brown scales in the silver spot at the end of interspace M_2; an extra silver spot at the margin in the same interspace; two minute silver spots on the anterior side of vein M_3; a black-encircled silver spot, a streak of brown, and three small brown spots next to the normal black spot in interspace Cu_1. On the right forewing, two small silver spots near the margin and vein M_2 in interspace M_1.

I believe this to be the first reported case of homoeosis in this species as no other records were cited by Sibatani (1983, A Compilation of Data on Wing Homoeosis in Lepidoptera. J. Res. Lepid. 22:1-46, 118-125) for the subfamily Heliconiinae.

Fig. 1. Homoeotic male *Agraulis vanillae incarnata*, ventral.
Fig. 2. Detail of ventral left forewing.

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A Complex Gynandromorph of *Pontia daplidice* (Pieridae)

A complex gynandromorph appeared in a brood of *Pontia daplidice* (L.) reared by H.-J. Geiger at the Zoologisches Institut der Universitat Bern, Switzerland, from a female collected September 18, 1963, at Gallargues-le-Montueux, 20 km SE Nîmes, France, by Prof. A. Scholl. The butterflies were reared under uncontrolled photoperiod and temperature. The specimen, which is in my collection at Davis, California, has a male left forewing, a female right forewing, a female left hindwing, and a mosaic right hindwing. The distribution of male and female tissue appears the same on both dorsal and ventral surfaces. The external genitalia are aborted but largely female and probably non-functional. The remainder of the brood was normal.

This specimen is the most complex mosaic gynandromorph known to me, presenting reversed sexual bilaterality in the fore- and hindwings, with anterior-posterior mosaicism on one hindwing, and all aspects repeated on both surfaces; nothing comparable to it was noted by Sibatani (1983, A Compilation of Data on Wing Homoeosis in Lepidoptera, J. Res. Lepid. 22:1-46). None of four developmental biologists I have consulted has been able to generate a reasonable hypothesis to account for it, though three have noted the distortion of shape in the male forewing and suggested it might be related to injury to the pupa. Unfortunately, the pupal exuviae were not saved.
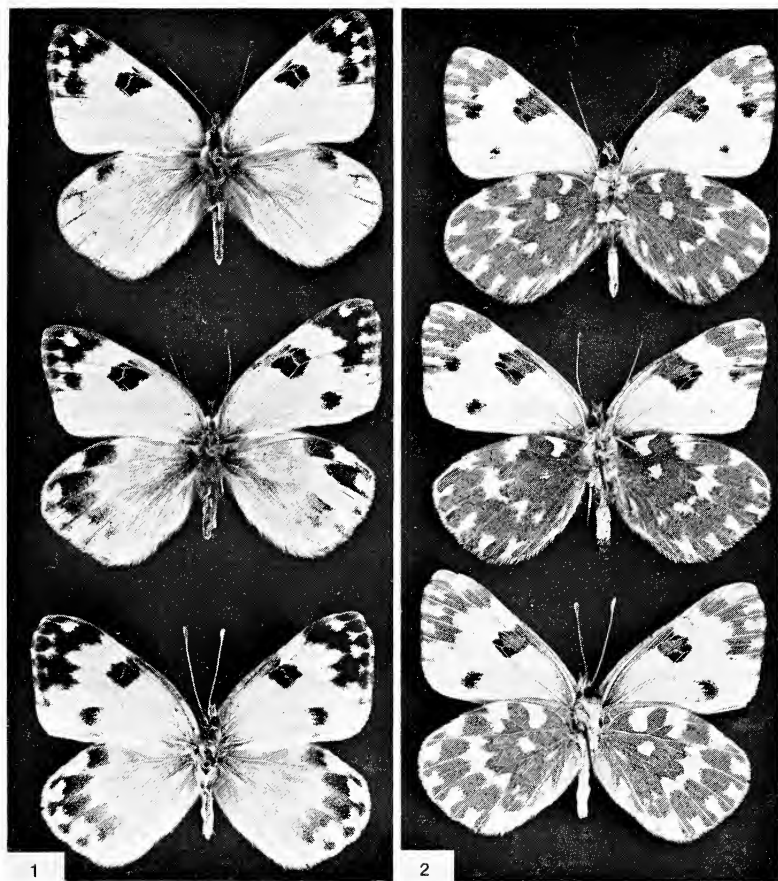
Fig. 1. Dorsal surfaces of *Pontia daplidice*. Top, normal male; center, gynandromorph; both from 20 km SE Nimes, France. Bottom, normal female, Ohrid, Macedonia, July 1969.

Fig. 2. Ventral surfaces of specimens in Fig. 1.

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The Origin of *Satyrium calanus albidus*

The recent paper on *albidus* (C. Ferris 1983, J. Res. Lepid. 21:188-193) did not mention the evolutionary reason for its pallidity. The strongly-white-underside *heathii* "aberration" is actually a recurrent *mutation* in hairstreaks (M. Fisher, J. Res. Lepid. 15:177-181). The pallidity of *albidus* must be due to several different genes, because variation is continuous between the whitest and darkest adults, and some populations (Montrose Co., CO) are rather pale, yet the whitest "*heathii*" forms are absent (or rare). In Man., Mich., or N.J. white mutants must be conspicuous to predators on the dark vegetation there, quickly spotted by predators. But everywhere I have found *albidus*, whitish-gray sagebrush (*Artemisia tridentata*) is common, on which adults frequently rest. When adults venture from the oaks out into the sage for feeding or mate-locating behavior, their whitish color camouflages them; for this reason, "*heathii*" mutants and the other less-pale mutants spread throughout the population. Subspecies *albidus* would be an ideal subject for the study of genetics and selection for camouflage, its one drawback being its single yearly generation. Interestingly, mate-locating behavior of *albidus* seems to differ from that of spp. *godarti*, occurring on ridgetops (J. Scott 1975, J. Res. Lepid. 14:16) versus gulches or depressions (Ferris' ridge populations may have similar behavior).

Ferris questions the validity of ssp. *albidus* because of its variability; actually it is valid simply because nearly all (at the type locality, all) adults are whiter than ssp. *godarti*, as Ferris amply demonstrates. Variability alone does not invalidate any taxon, witness *Colias eurytheme* and *philodice*, whose white females cannot be distinguished to species, *Papilio polyxenes coloro, zelicaon,* and *bairdii brucei,* whose variant forms are well known, and the ultraviolet variants within *Colias alexandra* subspecies described by Ferris himself. Variation is the working material of evolution, and geneticists now have proven that it is naive to expect *any* population to be invariant. The original description of *albidus* satisfies all the rules of Zoological Nomenclature, including those listed by Ferris, and the holotype, which resembles Figure 8 of Ferris' paper, is available for examination in the Los Angeles County Museum, as stated in the original description (Papilio 1:1-12, 1981). Some comments on types are required here because of misconceptions in Ferris' paper concerning the purpose of types. *Only* the holotype has any meaning in systematics, and *only* for the purpose of pinpointing the population from which it came—whether a holotype is an egg, cast larval skin, fossil impression, or the whitest "*heathii*" form (which it is not) does not invalidate the taxon, as numerous rulings attest—and the characteristics of the *population,* not the holotype, must be used for decisions regarding the validity of subspecies or species. Also, allotypes, paratypes, etc. have no validity or use whatsoever, except as syntypes from which a lectotype can be selected in the unlikely event that the holotype has been lost and a replacement is required (even in this case, a lectotype is "not to be designated as a matter of nomenclatorial convenience", as has occurred in the butterflies). But when such paratypes etc. are designated, to exclude "variants" from the type series would constitute bias.

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Book Reviews

Love Among the Butterflies: The Travels and Adventures of A Victorian Lady.
Cater, E. F., editor. 1980. Boston: Little, Brown and Company. 223 p. Price: $16.95.

She was found on a roadside in Trinidad in 1940, butterfly net in hand, dead at 78, having chased one last *Heliconius*. Truly a free spirit, a rugged individualist, Margaret Fountaine was a feminist long before it was a label. In the presence of this woman, ladies bristled while men fell all over themselves without a clue as to how best draw her omnivorous attention to them. And, dying as she lived, with a penchant for the dramatic, she left a locked box to be opened on the centennial of her birth. The box contained this book to be: a set of leather-bound diaries of a woman who roamed the world collecting butterflies at the time of Serbia and Austro-Hungary, and when Syria was Turkish.

The dustjacket, alas, promises considerably more than the book delivers, implying Henry Bates in or out of Anais Nin's clothing, or, perhaps, a blend of the *Malay Archipelago* and *Penthouse Forum*. *The Secret Life of a Victorian Lady* (inexplicably differing from the subtitle on the title page) is a rather generous assessment of the exploits of a woman who loses her virginity at the hardly tender age of 41. The jacket also subtly misleads by offering the Ceylonese *Papilio* and African *Acraea* against the backdrop of a diary page, indicating turn of the century adventures in the most exotic lands. Indeed, the color plates extend the theme, including *Callicore, Catagramma, Callithea* from the Fountaine collection, and *Charaxes* from Seitz's *Macrolepidoptera of the World*. But we only venture as far afield as North Africa and the Middle East until the virtual close of the book, when Jamaica and Sikkim break the circle of largely southern European escapades (nonetheless, keep in mind that Damascus or "Beyrout" of 1890 was more challenging to the visitor than Iquitos or Kinshasa would be today).

The butterflies, frankly, are a sideshow—the gimmick that allows the publication of another, and considerably inferior, version of *The Country Diary of an Edwardian Lady*. Butterflies are not the *raison d'etre* of the book, but more an odd manifestation of an eccentric spirit. And, sadly, one that the editor apparently finds terribly foreign. Commenting in the introduction on the effect of viewing the 22,000 specimens of the Fountaine collection, the editor clearly establishes his positon: "They are a beautiful but—again to the layman—a slightly chilling sight, so much dead brilliance." That level of appreciation is reflected throughtout, as butterflies suffer from a decidedly subordinate position to Miss Fountaine's assorted "lovers."

The latter are a collection as well: a chorister, a hotelkeeper's son, an Italian baron, a "wild gipsy-looking fellow", a snow-blinded Swiss physician, an Egyptian ship's officer, several "wayward boys", a couple of aristocratic British sportsmen (read ne'er-do-wells looking to beef up their inheritance with hers), and, ultimately, her Syrian boy Friday-come-husband. These "lovers", as she refers to them, are only such in the most liberal of interpretations. Her intercourse with them ranges from battling leers in railroad cars to avoiding parting kisses by ducking under bedclothes; at no point until the Syrian are "lovers" in fact lovers.

While neither the butterflies nor the lovers are likely to satisfy, the book nevertheless is entertaining, if not enthralling. Her writing is quite inspired in parts, and although not particularly quoteworthy, the descriptions are full, rendering the feeling and spirit of the time and places. The mixing of Victorian past and the surprisingly modern is enlightening. Lebanon still sported cedars in 1901, but "there was no shade at all along the lower slopes of Mount Hermon. . .the Turks cut down all the trees for profit, and made Syria the thirsty land it is. . ." Or, in 1908, she notes that ". . .civilization already has a foot on the shores of the Zambesi and the hippos and crocodiles once abundant are rarely seen." And, of Malaya, "too much rubber planting. . .for beauty or for butterflies."

However, it is of herself that Miss Fountaine paints the richest and most complex picture. From teenage entries on, she is remarkably self-aware albeit rarely self-satisfied. Consistently honest to the point of self-deprecation, she struggles with her position in society, the parade of men in her life, and her turmoil as a strong and independent woman suffering bouts of loneliness and helplessness. She is disarmingly candid about her physical attributes (and lack thereof) and those of others. Through the heat, the dust, and the fleas, she remains captive to what she views as "the usual stiffness of English manners", both in her daily protocol and a doggedly adhered-to sense of position in an absolute hierarchy from which one simply does not descend.

We are chided by the editor "to remember that Miss Fountaine was born four years before the end of the American Civil War into a world where belief in racial equality was rare to the point of eccentricity. . ." Indeed, she spares no quarter in her assessments of those on the road, from noisy Germans to aggravating Orientals to "Soudanese perfectly black and evil looking". But her flurries have no racial boundaries and her own countrymen take an equal share of criticism, portrayed as intoxicated, ambitionless blokes well on their way to losing an empire. True spite, though, is saved for her unsuccessful suitors; even her one true love, of sorts, remains more servant or "dragoman" than mate, marriage simply serving to expand his job description.

Since the match of text to diary is not exact (as we can see from the plate opposite page 137), one wonders just how many liberties have been taken by the editor, a censor who also felt it necessary to italicize "diurnal lepidoptera". And yet, despite not much love, really not that many butterflies, and a self-aggrandizing lead-in by Miss Fountaine "to the reader, maybe yet unborn, I leave this record of the wild and fearless life. . .", there are just enough Ceylonese zealots, Arab nihilists, and Buddhist funeral pyres to keep our attention. Perhaps its highest achievement is that the book reads so smoothly that we easily forget that it is a personal diary, and was not actually meant to end up on our end tables.

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INSTRUCTIONS TO AUTHORS

Manuscript Format: **Two** copies *must* be submitted (xeroxed or carbon papered), double-spaced, typed, on 8½ x 11 inch paper with wide margins. Number all pages consecutively and put author's name at top right corner of each page. If your typewriter does not have italic type, underline all words where italics are intended. Footnotes, although discouraged, must be typed on a separate sheet. Do not hyphenate words at the right margin. All **measurements** must be metric, with the exception of altitudes and distances which should include metric equivalents in parenthesis. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as example: 4. IV. 1979 (day-arabic numberal; month-Roman numeral; year-arabic numeral). Numerals must be used before measurements (5mm) or otherwise up to number ten e.g. (nine butterflies, 12 moths).

Title Page: All papers must have the title , author's name, author's address, and any titular reference and institutional approval reference, all on a separate title page. A **family citation must** be given in parenthesis (Lepidoptera: Hesperiidae) for referencing.

Abstracts and Short Papers: All papers exceeding two typed pages must be accompanied by an abstract of no more than 300 words. An additional summary is not required.

Name Citations and Systematic Works: The first mention of any organism should include the full scientific name with author (not abbreviated) and year of description. New descriptions should conform to the format: male: female, type data, diagnosis, distribution, discussion. There **must** be conformity to the current International Code of Zoological Nomenclature. We strongly urge deposition of types in major museums, all type depositions must be cited.

References: All citations in the text must be alphabetically listed under Literature Cited in the format given in recent issues. Abbreviations must conform to the *World List of Scientific Periodicals.* Do not underline periodicals. If four or less references are cited, please cite in body of text not in Literature Cited.

Tables: Tables should be minimized. Where used, they should be formulated to a size which will reduce to 4 x 6½ inches. Each table should be prepared as a line drawing or typed with heading and explanation on top and footnotes below. Number with Arabic numerals. Both horizontal and vertical rules may be indicated. Complex tables may be reproduced from typescript.

Illustrations: Color must be submitted as a transparency (i.e., slide) ONLY, the quality of which is critical. On request, the editor will supply separate detailed instructions for making the most suitable photographic ilustrations. Black and white photographs should be submitted on glossy paper, and, as with line drawings, must be mounted on stiff white cardboard. Authors **must** plan on illustrations for reduction to the 4 x 6½" page. Allowance should be made for legends beneath, unless many consecutive pages are used. Drawings should be in India ink at least twice the final size. Include a metric scale or calculate and state the actual magnification of each illustration as printed. Each figure should be cited and explained as such. The term "plate" should not be used. Each illustration should be identified as to author and title on the back, and should indicate whether the illustration be returned.

Legends should be separately typed on pages entitled "Explanation of Figures". Number legends consecutively with separate paragraph for each page of illustrations. Do not attach to illustrations. Retain original illustrations until paper finally accepted.

Review: All papers will be read by the editor(s) & submitted for formal review to two referees. Authors are welcome to suggest reviewers, and if received, submit name & comments of reviewers.

THE JOURNAL OF RESEARCH

ON THE LEPIDOPTERA

IN THIS ISSUE

COVER ILLUSTRATION: Devils Tower National Monument, Wyoming, showing a typical collecting site in the oak-pine transition belt, see Ferris, p. 297.

THE JOURNAL

OF RESEARCH

ON THE LEPIDOPTERA

Invited Paper

Butterfly Thermoregulation: Organismic Mechanisms and Population Consequences

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Introduction

Many butterflies regulate their body temperatures in order to meet the thermal requirements for flight. Thermoregulation in butterflies is of interest at two different but complementary levels. First, the physiological and behavioral mechanisms by which Lepidoptera regulate their body temperatures are arguably the most diverse in any group of insects. Second, because of the importance of flight in butterfly biology, thermoregulation provides a vital link relating weather to the population ecology of butterflies.

This review will focus on these two aspects of thermoregulation. Rather than provide a comprehensive summary of thermoregulation in all butterflies studied to date, I shall try to provide a conceptual framework by which to categorize the diversity of thermoregulatory characteristics in butterflies. As a counterpoint to the patterns found in butterflies, I shall also briefly describe the mechanisms of thermoregulation in moths and other insects. I shall use this framework to examine the relation of weather, body temperature, and flight. Finally, I shall summarize recent work in butterfly demography that illustrates the importance of thermoregulation and flight in the population ecology of butterflies.

Mechanisms of Thermoregulation

Most butterflies appear to require elevated body temperatures in order to fly. A survey of 40 species of temperate US butterflies showed that the preferred thoracic temperatures during flight were between 30° and 39°C (Douglas, 1978). (Since the flight muscles are in the thorax, thoracic temperature is the most directly relevant to flight.) More detailed studies of *Papilio* (Rawlins, 1980), *Colias* (Watt, 1968), and *Pieris* (Kingsolver, in press) confirm that thoracic temperatures between 28 and 42°C are required for flight, with rigorous flight restricted to the 33-38°C subrange.

Thus, butterflies appear to be quite similar in their body temperature requirements for flight. These temperatures are similar to those found in many other thermoregulating insects, although slightly lower than those in large moths and in bumblebees (Heinrich, 1981). What are the means by which butterflies achieve and maintain these elevated body temperatures?

Because body temperature is the result of a balance between the rates of heat gain and heat loss, there are two ways of regulating an elevated body temperature: regulation of heat gain, and regulation of heat loss. In addition, there are two different levels at which this regulation of heat gain and loss can occur: regulation of heat production and heat transfer within the body (physiological mechanisms); and regulation of heat exchange between the body and the external environment (behavioral mechanisms). We shall examine both physiological and behavioral mechanisms of thermoregulation, and show how regulation can occur in both heat gain and heat loss.

Physiological Mechanisms

One means of heat gain for thermoregulation is by the metabolic generation of heat, called endothermy. In insects, this heat production results largely from the activity of the thoracic flight muscles, and can occur both during flight and during preflight warmup. During preflight warmup, the muscles that are antagonistic during flight (the wing elevator and wing depressor muscles) are activated simultaneously. These isometrically contracting muscles thus produce heat but little wing movement.

Endothermic heat generation during preflight occurs in a variety of moths, including Saturniids (Kammer, 1968), Sphingids (Heath and Adams, 1967; Kammer, 1970b), and Geometrids and Noctuids (Casey and Joos, 1983), but appears to be quite uncommon in butterflies. The only butterfly reported to date to consistently use endothermic preflight warmup is *Danaus plexippus* (Kammer, 1970a). In *Papilo* preflight endothermy also occurs occasionally, but only in disturbed individuals under conditions too cool for flight (Rawlins, 1980). In both *Papilio* and *Danaus*, endothermy is less effective than behavioral means for increasing body temperature.

During flight, heat is produced by the rapid contraction of flight muscles. Heat production during flight under conditions of low solar radiation has been shown to raise thoracic temperatures by 3-6°C in a number of butterflies, including *Papilio* (Rawlins, 1980), *Danaus* (Kammer, 1970b), and *Colias* (Tsuji *et al.*, in prep.). In contrast, many moths, particularly large Sphingids and Saturniids, achieve thoracic temperatures during flight of 10-20°C above air temperature (Heath and Adams, 1965; Heinrich, 1971; Heinrich and Casey, 1973; Bartholemew and Epling, 1975).

Because the flight muscles are in the thorax, it is thoracic temperature

that is generally regulated most precisely. A variety of studies have documented that insects do not regulate abdominal temperature as precisely as thoracic temperature during flight. The transfer of heat between thorax and abdomen can, however, affect thoracic temperature. One physiological means of regulating this heat transfer is to regulate the circulation of hemolymph.

This mechanism, which has been described for a number of large moths and bees, has been explored in detail in *Manduca sexta* (Heinrich, 1971). During endothermic preflight warmup, thoracic temperature rises rapidly, but abdominal temperature remains near ambient air temperature. During flight at low air temperature, abdominal temperature remains near ambient, but at high air temperatures the abdominal temperature is nearly as high as thoracic temperature. This means that at low air temperature the abdomen loses little heat, but at the high temperature heat loss from the abdomen is substantial (Kammer, 1981).

These patterns result from the hemolymph flow between thorax and abdomen. At high air temperatures the rate of heartbeat is high and the hemolymph flow is rapid. Heat generated in the thorax is rapidly transferred to the abdomen, which is poorly insulated and loses heat rapidly. At low air temperatures the heart and hemolymph flow rates are low, and little heat is transferred and lost through the abdomen. This provides a rather precise mechanism for regulating heat loss and thus thoracic temperature.

While this mechanism occurs in large Sphingid and Saturniid moths, it has not been described in butterflies. The most detailed study to date for thermoregulation during flight in butterflies found no evidence for hemolymph flow regulation (Tsuji *et al.* in prep.). Rawlins (1980) has described abdominal pumping in restrained *Papilio polyexenes* at high air temperatures, which resulted in increased heat loss, but the quantitative importance of this mechanism under natural conditions is unclear.

Another potential means by which hemolymph circulation could affect heat loss is flow in the wing veins. Clench (1966) suggested that hemolymph flow in the wing veins could facilitate heat transfer between the wings and thorax, and contribute to thoracic heating. However, all studies of basking to date refute this hypothesis (Watt, 1968; Wasserthal, 1975; Douglas, 1978). Recent careful measurements of hemolymph flow rates in the wing veins indicate that, at rest, these flow rates are far too slow to significantly affect thoracic temperature (Wasserthal, 1984). The possibility that more rapid flow in the veins during flight could enhance heat loss remains, but this hypothesis will be difficult methodologically to test.

In summary, physiological mechanisms such as preflight endothermy and regulation of hemolymph circulation do not appear to be of general importance in butterflies, while they do occur in many moths and other

insects. Recent mathematical models of heat exchange suggest that, because of the relatively slender body and poor insulation in butterflies, endothermy is simply too expensive energetically (Tsuji *et al.* in prep.). Butterflies rely instead on a variety of behavioral mechanisms for thermoregulation.

Behavioral Mechanisms

The principal way that butterflies regulate heat gain is by behavioral orientation and posture relative to the sun, called basking. Detailed behavioral studies of basking began in the 1950's (Vielmeter, 1954, 1958), and Clench (1966) proposed a classification of basking postures based on wing position. We can describe basking posture in terms of a body orientation angle relative to the sun, and a wing angle (Fig. 1). Using these we can categorize the different basking postures of butterflies (Fig. 2). In dorsal basking, the dorsal surfaces of the thorax and of the wings are positioned perpendicular to the sun ($\Upsilon = 0°$, $\theta = 90°$). In lateral basking the wings are folded tightly over the dorsum and orient the body and ventral wing surfaces perpendicular to the sun ($\Upsilon = 90°$, $\theta = 0°$). Body basking posture is similar to dorsal basking except that at least the forewings are only open at a small angle ($\Upsilon = 0°$, $\theta \geq 5°$).

In body basking, which occurs in Lycaenids and many skippers, the body directly absorbs solar radiation. In the other basking postures, the wings contribute to radiation interception and heat gain. For these postures, wing position and wing color have important thermal effects, which we shall consider in detail.

The physical mechanisms of heat transfer during dorsal basking have been studied in *Papilio*. Wasserthal (1975) showed that the presence of wings could increase the thoracic temperature excess above ambient air temperature by 40-50% in *Papilio*, and that most of these thermal effects are produced by the basal parts of the wings within 5-10 mm of the thorax. These effects appear to be due to two mechanisms. First, radiation is absorbed by the dorsal, basal wing surfaces and the heat is conducted along the wing to the thorax. Because the wing is a relatively poor conductor of heat, only the parts of the wing within a few mm of the thorax can contribute to this process (Kingsolver and Koehl, in press). Second, warm air heated by the wings and body can accumulate beneath the wings, reducing convective heat loss from the thorax (Douglas, 1978). The relative importance of these mechanisms probably depends on wind speed, the latter mechanism dominating at low wind speeds.

Rawlins' (1980) detailed study of dorsal basking in *Papilio polyxenes* also demonstrates the importance of abdomen position relative to the hindwings. During basking, the abdomen is raised above the wings, and is exposed to direct solar radiation. At high ambient temperatures, however, the abdomen is positioned below and shaded by the wings,
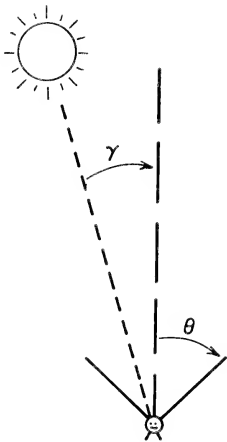
θ : Wing Angle

γ : Orientation Angle

Fig. 1. Diagram illustrating the definitions of body orientation angle (γ) and wing (θ) during basking. From J. G. Kingsolver (1985a), Oecologia, in press.

Basking Postures

$\theta = 0°$ $\theta = 90°$ $5° < \theta < 90°$
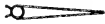
$\gamma = 90°$ or $270°$ $\gamma = 0°$ $\gamma = 0°$

Lateral   Dorsal   Reflectance

Fig. 2. Diagram illustrating several common basking postures of butterflies. From J. Kingsolver (1985a), Oecologia, in press.

reducing radiation load and increasing convective heat loss from the wind. In addition, at high temperature the angle of the wings (θ) decreases, and the body orientation becomes nearly random, reducing radiation load.

Dorsal basking is found in many species of Nymphalids, Danaiids, Papilionids, and Heliconiids (Douglas, 1978). A variation of dorsal basking, termed conduction basking, occurs in *Parnassius* and perhaps in other alpine and artic butterflies found in rocky or bare-ground habitats. In conduction basking, the wings are open and the body and ventral wing surfaces are oppressed to the ground, trapping warm surface air and conducting heat from the substrate to the body.

Perhaps the most comprehensive examination of the role of orientation and wing color in butterfly thermoregulation has been in the laterally basking *Colias* by Watt (1968, 1969) and associates (Hoffman, 1974; Tsuji, 1980; Kingsolver, 1983a; Kingsolver and Moffat, 1982; Kingsolver and Watt, 1984). As body temperature increases, *Colias* change their body orientation relative to the sun from perpendicular to random to parallel. During lateral basking the basal parts of the ventral hindwing absorb radiation, and heat is conducted along the wing to the thorax. The proportion of black, melanin scales on the basal, ventral hindwings determines the butterfly's solar absorptivity (defined as the fraction of radiation striking the butterfly which is absorbed by it), and affects thoracic temperature. There is variation among species, and among seasons within species, in the degree of hindwing melanization; in addition in some species temperature and photoperiod conditions during the larval stages can influence adult wing melanization. The result of this variation is that *Colias* occurring in colder habitats have increased melanization; and highly melanized forms can achieve body temperature excesses above air temperature of 15-80% greater than lighter forms. These results are the clearest demonstration of the adaptive significance of wing or body coloration in thermoregulation of insects.

A similar case of photoperiodic effects on melanization for thermoregulation occurs in the lateral basker *Nathalis iole* (Douglas and Grula, 1978). This system of environmental determination of melanization has been implicated in the recent range expansion of this species. Lateral basking is common among Pierids (Coliadinae), and is found in some Lycaenids, Satyrids, and Hesperiids.

There have been no detailed thermal studies of body basking, although it is quite common in Lycaenids, Satyrids, and Hesperiids. It is not clear that radiation absorption by the wings has any thermoregulatory effects in body baskers. It may be that the wing position functions largely to reduce convective heat loss by altering air flow patterns around the body.

A novel basking posture recently described in *Pieris* butterflies

(Kingsolver, in press a, b) is known as reflectance basking (Fig. 2). In this behavior the dorsal thorax is oriented toward the sun ($\gamma = 0°$), and the white wings function as solar reflecting plates that reflect radiation to the body. A detailed examination reveals some non-intuitive relationships between the wing angle used during basking, wing color pattern, and body temperature. For example, if we consider this reflection process from the wings, we can show that the wing angle during basking determines those regions of the wings that can contribute to reflection to the body (Fig. 3). Kingsolver (in press b) developed and tested a mathematical model of reflectance that predicted that butterflies would achieve maximum body temperature at some intermediate basking wing angle, and that the wing angle producing this maximum depends on the extent of melanization at the dorsal margins of the wings. This model correctly predicts that *Pieris* in the subgenus *Pontia*, which have extensive dorsal marginal melanization, achieve maximum body temperatures at and use larger wing angles during basking than those in the subgenus *Artogeia*, which have little
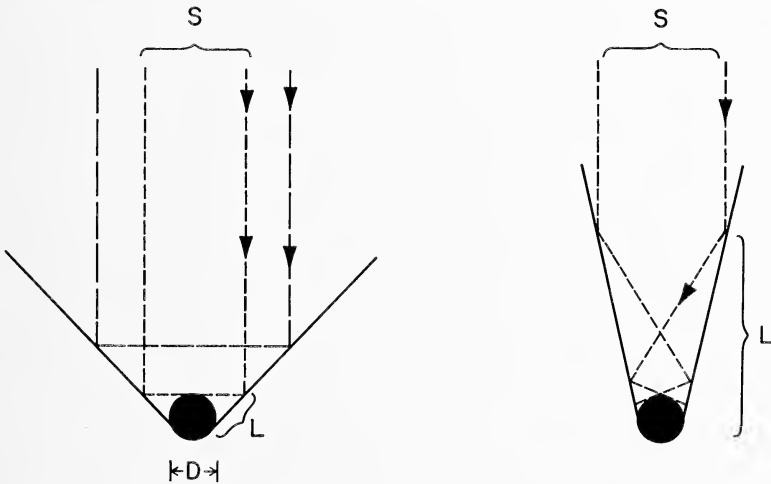
Fig. 3.   Diagram illustrating the reflection of solar radiation from the wings to the body in *Pieris*. The butterfly is considered as a black, cylindrical body with white, flat plates as wings; the figure shows a cross-section through the butterfly perpendicular to the body axis. *D* is the diameter of the body. Beams of radiation (dashed lines) approach the butterfly from above and reflect off the wings. Radiation striking the wings near the body is reflected onto the body, increasing body temperature; radiation striking farther out on the wings is reflected away and does not reach the body. The region of the wings (*L*) that contributes to reflecting radiation to the body is smaller at large wing angles (left panel) than at small wing angles (right panel). From J. G. Kingsolver (1985b), Oecologia, in press.

dorsal marginal variation; the model also correctly predicts behavioral differences in basking between male and female *Pontia*.

These results for reflectance basking are of general interest for two reasons. First, they represent the first demonstration in any insect that the pigmentation pattern on the entire wing surface may be relevant to thermoregulation. Second, reflectance basking requires highly reflective wings: increased melanization in some wing regions can actually decrease body temperature. This effect of melanization is precisely the opposite of that in *Colias, Nathalis,* and other butterflies that use their wings to absorb radiation. Thus, the function of melanization in butterflies depends on the behavioral mechanisms of thermoregulation. Shapiro (see 1976 for a review) and Bowden (1979) have summarized the correlations between climate and melanization, and the environmental determination of melanin deposition, in *Pieris*. These results on reflectance basking suggest that Bowden's (1979) conclusion that most sub-specific variation in the *P. napi* complex is non-adaptive, while perhaps correct, is premature; a more detailed functional analysis will be required.

While, as noted above, several workers have identified particular mechanisms of heat loss that influence body temperature for dorsal baskers (Douglas, 1978; Rawlins, 1980), there have been few systematic studies of the behavioral regulation and determinants of heat loss in butterflies. To date only two systems have been documented in detail: the laterally basking *Colias*, and the dorsally basking *Vanessa cardui*.

Kingsolver and Moffat (1982) examined convective heat loss from real and model *Colias* in a wind tunnel, varying both wind speed and wind direction (yaw angle). Their results indicated that there was no significant effect of wind direction on heat loss, and that the air trapped above the body by the closed wings acted as an insulation layer, reducing heat loss. They also demonstrated that the pubescence on the ventral thorax reduced convective heat loss by 10-70%, and that differences in the thickness of ventral pubescence generated differences in convective heat loss. There are significant differences in the thickness of ventral pubescence among *Colias* species along an elevational gradient in Colorado (Kingsolver, 1983a), with thicker pubescence at higher elevations.

In his wind tunnel study of *Vanessa (Cynthia) cardui*, Polcyn (1984) systematically varied wind direction, wing angle, and the direction of artificial radiation and observed the resulting changes in thoracic temperature excess over air temperature. He showed that wind direction significantly affected body temperature excess, with heat loss being smallest when the tip of the abdomen faced into the wind (i.e., yaw angle = 180°). This effect of wind direction was strongest for dorsal basking and weakest for lateral basking posture. The results suggest that wind direction has larger effects on thoracic temperature than the radiation direction in *Cynthia*, at least for the rather low radiation conditions considered

in the study.

Despite Polcyn's results, there is at present no solid evidence that butterflies behaviorally orient to wind direction (except at high wind speeds, where the response is more likely a mechanical than a thermoregulatory one) in the lab and the field, even in the careful field studies by Watt (1968) and Douglas (1978). However, in many instances this lack of evidence may largely reflect the difficulties of detecting orientation to wind in the field.

In summary, butterflies largely rely on behavioral means of thermoregulation, principally on wing and body orientation to the sun. For at least certain well studied sytems, we now have a quantitative understanding of the mechanisms of heat loss and heat gain that occur for each major basking posture, except for body basking. Wing color and melanization at the wing bases can play an important role in thermoregulation in lateral and dorsal baskers. Reflectance basking in pierines provides a unique case in which the entire dorsal wing pigment pattern can affect body temperature, and in which the thermal effects of melanization can be opposite of that in other butterflies. This suggests that we cannot determine the thermal significance of wing pigment pattern without a detailed understanding of the physical and behavioral mechanisms of thermoregulation. Pubescence on the thorax has been shown to decrease heat loss, and there are significant differences in the thickness of pubescence among some congeners that influence body temperature. While there is no evidence that butterflies behaviorally orient to wind for thermoregulation, recent conflicting results suggest the potential effectiveness of wind orientation in at least some butterflies.

Weather, Thermoregulation, and Ecology

The Flight Space

Because flight is a temperature-dependent process in butterflies, weather can influence the occurrence and degree of flight in the field. The relationship between weather and flight can be summarized by using the concept of a flight space. The flight space is defined as the ranges of certain meteorological variables, such as solar radiation, air temperature, and wind speed, in which flight can or does occur in a particular butterfly or species of butterfly. Flight spaces have been empirically evaluated in the field for a number of butterflies, including *Papilio polyxenes* (Rawlins, 1980), *Colias nastes* (Roland, 1982), *Colias philodice eurytheme* (Leigh and Smith, 1959), and *Pieris virginiensis* (Cappuccino and Kareiva, 1985), and reveal considerable differences in flight space among species. For example, flight in *Papilio polyxenes* is limited to air temperatures between 19° and 30°C, while in *Colias nastes* flight occurs between 6 and 20°C. Because these butterflies have similar ranges of body

temperatures for flight, the differences in flight space presumably result from differences in thermoregulatory characteristics and mechanism. Roland (1982) also showed that the degree of hindwing melanization in *C. nastes* is correlated with the lower limit of solar radiation at which flight occurred. In addition, he demonstrated that certain behavioral activities such as courting and oviposition only occurs in restricted regions of the flight space.

Purely empirical investigations of flight space are essential, but at best represent a subset of the entire space. First, the range of weather conditions observed in a particular population or species may cover only a part of the flight space. This limitation can be overcome by transplanting butterflies to sites with different weather conditions (Kingsolver and Watt, 1984). A second, more fundamental limitation is that such empirically-derived flight spaces give little information about the factors determining the size, shape, and position of the flight space. A more general approach is to develop and test models that link thermoregulation to the flight space.

This approach has been used in some detail for *Colias* by Kingsolver (1983a, 1983b; Kingsolver and Watt, 1983, 1984), and is based on the fact that body temperature (T_b) is determined by the balance of the rates of heat inputs (E_{in}) and heat outputs (E_{out}):

$$E_{in} = E_{out} \tag{1 a}$$
$$E_s = E_c + E_t \tag{1 b}$$

where E_s is the rate of solar radiative heat gain, and E_c and E_t are the rates of convective and therman radiative heat loss, respectively. Because E_c and E_t depend on body temperature, equ (1) can be solved to show that body temperature is a function of certain meteorological variables (air and ground temperature, wind velocity, solar radiative load) and certain characteristics of the butterfly (wing color, wing and body area, behavioral orientation, pubescence, and a heat loss coefficient that depends on the size, shape, and position of the butterfly). If we can quantify these butterfly characteristics, we can then predict body temperature under specified meteorological conditions, and use this to identify the set of meteorological conditions in which a given butterfly can achieve the body temperatures needed for flight: i.e., the flight space. Such models have been successfully developed and tested by predicting and then measuring the diurnal patterns of body temperature and flight in several *Colias* populations (Kingsolver, 1983a).

This modeling approach to the study of flight spaces has several advantages. First, one can look at how the differences in thermoregulatory characteristics among species determine the differences in flight spaces. For example, the flight spaces of *Colias philodice eriphyle* and *Colias meadii* differ by about 20%, mainly as a result of the more heavily melanized ventral hindwings of *meadii* (Fig. 4a). Second, one can use the
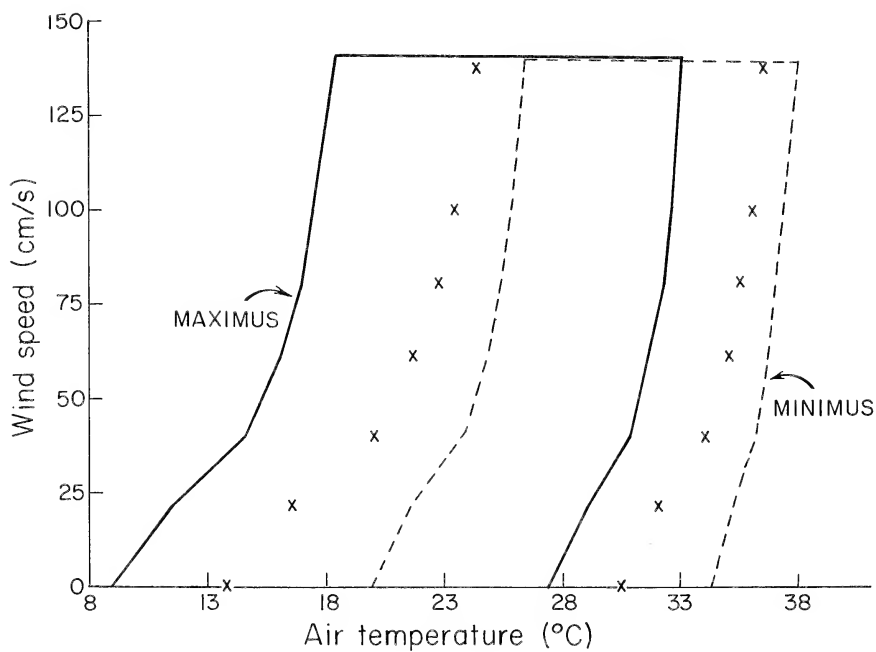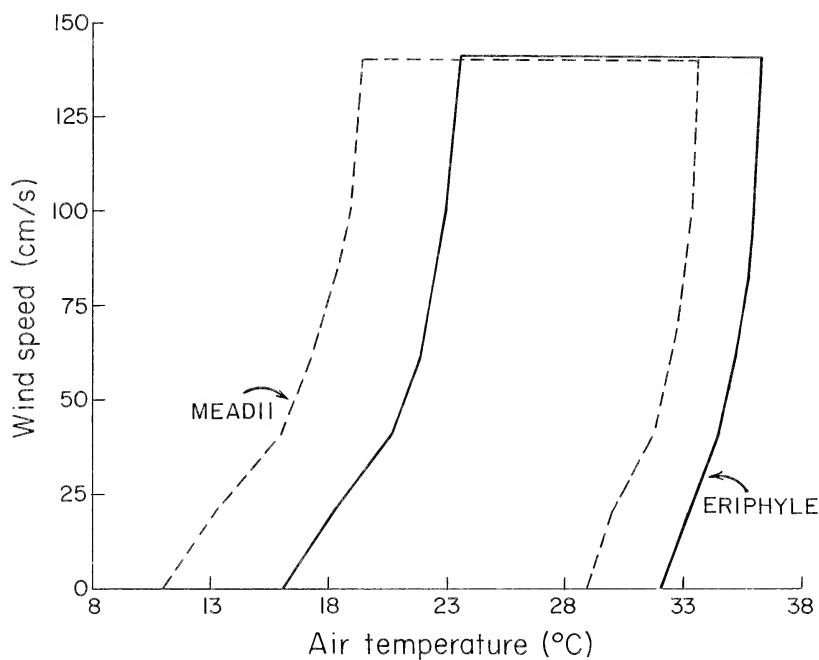
Fig. 4.   Flight space diagrams based on model simulations as a function of wind
          speed (cm/s) and air temperature (°C) for several *Colias* butterflies.
          Solar radiation load perpendicular to the solar beam is 110 mW/CM^2.
          The area enclosed by the lines is the flight space (see text). From
          Kingsolver, J. G. (1983a), Ecology 64:534-545.

          a) *Colias meadii* (dashed line) from Hinsdale Co., Colorado (elevation
          3.6 km) and *C. philodice eriphyle* (solid line) from Montrose Co.,
          Colorado (elevation 1.7 km).

          b) Two hypothetical *Colias* species: *C. maximus* (solid line), with all-
          black wings, back, and a thick pubescence layer; and *C. minimus*, with
          all-yellow wing bases and no thoracic pubescence. The flight space for a
          form with all-black wings and no pubescence (X) is also indicated.
          See text.

flight space to predict the patterns of flight space for a particular species
in various weather conditions. For example, the model predicts that *C. p.
eriphyle* transplanted to the typical habitat of *C. meadii* would not
achieve consistent flight at all—it simply could not achieve the necessary
body temperatures for flight. Actual transplant experiments confirm this
prediction (Kingsolver and Watt, 1984). Finally, one can use the model to
systematically explore the effects of thermoregulatory characteristics
such as wing solar absorptivity on the flight space. For example, wing
color (and absorptivity) in *Colias* is determined by a mixture of two pig-
ment systems: a black, melanin pigment, and a yellow-orange pteridine
pigment mixture. Consider two imaginary, extreme *Colias* 'species': *C.
minimus*, a butterfly with all-yellow wings and no thoracic pubescence,
and *C. maximus*, a butterfly with all-black wings and a thick pubescence
layer. Using the model to generate the flight spaces for these imaginary
'species' (Fig. 4b), one can show that the overlap in flight space is less
than 40%, demonstrating the wide range of meteorological conditions to
which *Colias* can adapt using a rather simple system of thermo-
regulation.

The above discussion of flight space implies that meteorological con-
ditions do not change rapidly relative to the response of the butterfly. In
fact, in many outdoor environments radiation, air temperature, and wind
speed can all change considerably over quite short time periods. Because
of the small size and mass of a butterfly, its body temperature can change
dramatically in 30-60s. As a result, meteorological variation on a time
scale of one to a few minutes are of great importance to insects in general,
and butterflies in particular.

While a number of workers have noted the rapid thermal response of
butterflies, there are few systematic studies of the effects of such varia-
tion for thermoregulation and flight. At the low end of the flight space,
brief periods of cloudiness can drastically reduce flight activity (e.g.
Kingsolver, 1983a). At the high end, brief periods of low wind and/or high

temperature can quickly lead to overheating in butterflies, and it has been shown that such overheating can lead to decreased survivorship and fecundity (Rawlins, 1980; Kingsolver and Watt, 1983). Lederhouse (1982) has shown how such intermittent overheating can force *Papilio polyxenes* males to abandon their defended mating territories. Kingsolver and Watt (1983) have shown that short-term meteorological variation consistently leads to brief periods of overheating and flight cessation in *Colias* butterflies, even at elevations above 3500 m with cool 'average' conditions. These studies suggest that such short-term effects may be of considerable biological importance, and will profit from further investigation.

Thermoregulation and population ecology

Beyond the consequences of overheating for survivorship, fecundity, and territorial defense discussed above, the principal ecological effects of thermoregulation involve the relation of weather to flight activity. These effects can be expressed either in survivorship or fecundity.

The inability to fly because of weather conditions may be an important component of mortality due to predation on adult butterflies. Lederhouse (1983) demonstrated a weather-related increase in mortality in *Papilio polyxenes* that was associated with roosting. Bowers *et al.* (1984) presented evidence based on beak marks for increased bird predation on *Euphydryas chalcedona* that was correlated with unusually cool and cloudy weather. These results suggest that butterflies may be most susceptible to predation during roosting and basking periods when they are unable to attain the body temperatures needed for vigorous flight. However, field experimental tests of this hypothesis have yet to be done.

The relationship of weather, thermoregulation, and realized fecundity has been more closely examfined. In fact, this relationship may play an important role in the population ecology of many temperate butterflies. As a result, we shall consider the determinants of realized fecundity in some detail.

A principal mechanism by which weather and thermoregulation influences fecundity is through limitations on the time available for oviposition activity, which has been examined in some detail for *Colias* in the Colorado Rocky Mountains (Kingsolver, 1983a, b). Along an elevational gradient, there are significant differences among *Colias* populations in the amount of time available for flight activity. Because of the short adult lifespan (4-5 days: Watt *et al.* 1977, 1979; Tabashik, 1980), *Colias* in the higher elevation populations may average only 12-15 h of available flight time during their entire adult lives. Because female *Colias* lay eggs singly on host plants, and need to fly between plants, sufficient flight time is required to locate host plants and lay a full complement of eggs (the maximum fecundity of these species is about 700-1000

eggs: Tabashnik, 1980). In fact, by combining field data on available and realized flight time, activity budgets, longevity, and maximum oviposition rates, Kingsolver (1983b) estimated that *Colias* females in high elevation population can lay only 20-50% of their full complement of eggs as a result of limited flight time.

This suggestion that limited flight time can reduce realized fecundity is supported by several lines of evidence. Flight cage experiments have shown that daily egg production is closely correlated with solar radiation and air temperature in *Pieris rapae* (Gossard and Jones, 1977). Studies with *Colias philodice eurytheme* in environmental chambers showed strong effects of air and body temperature on ovipositon rate (Stern and Smith, 1960). More generally, Courtney (1984) has recently summarized field data on realized fecundity for insects. For Lepidoptera that lay eggs singly, the mean realized fecundity was less than ⅓ of the maximum for all species reported. This strongly suggests the importance of thermoregulation and flight time for fecundity.

An alternative mechanism by which thermoregulation and weather could affect realized fecundity is by influencing the rate of egg maturation (S. Courtney, pers. comm.). Egg maturation rate is a temperature-dependent process in many insects (Wigglesworth, 1972), and thermoregulation by females could increase the maturation rate. While no data are yet available on this possibility in natural conditions, lab and field cage experiments suggest that egg maturation is one component determining oviposition rate (Gossard and Jones, 1977; Stern and Smith, 1960).

The relationship between weather, flight, and fecundity provides us with a useful tool to explore the factors determining the population dynamics of butterflies. In particular one can ask, how does temporal variation in weather affect variation in fecundity and in population size?

One can use the models described above that relate weather to flight time to address this question with the following thought experiment. Consider a female butterfly that emerges on a given day during the flight season, lives and (potentially) lays her eggs during a five-day period, and then dies. What is the expected lifetime flight time available to her? I have used models developed for *Colias* (Kingsolver, 1983a) and solar radiation and air temperature data (mechanical pyranograph and thermograph) from Gothic, Colorado (elevation 2.9 km) to simulate this situation for female *Colias alexandra* in a univoltine population in Gunnison Co., Colorado (Hayes, 1981). The frequency distribution of expected flight time (in hours per five-day lifetime) shows that there is considerable variation within years during a flight season, and between years (Fig. 5). In some years, up to 25% of the population may have 25-30 h of flight time; in other years, 10% of the populations may have less than 5 h. This
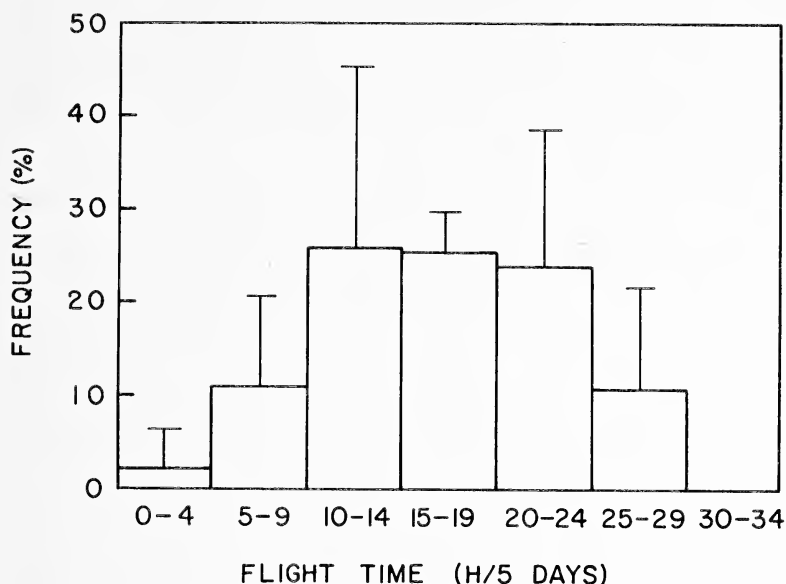
Fig. 5. Frequency distribution of the expected available flight time (in hours per 5-day lifetime) for *Colias alexandra* females in Brush Creek near Crested Butte, Colorado (elevation 2.9 km). The histogram is estimated using the model of Kingsolver (1983a) and solar radiation and air temperature data from Gothic, Colorado, for the month of July (the flight season of *C. alexandra* at this site) for the period 1973-1982. Error bars represent standard deviations of variation among years.

flight time variation would have large effects on variation in realized fecundity both within and between generations. Thus, variation in realized fecundity due to weather variation could affect population fluctuations.

This suggestion that weather and population fluctuations are related *via* flight time and fecundity is supported by a recent review of demographic studies of Lepidoptera by Dempster (1983). He summarized available studies on temperate zone Lepidoptera in which key factor analysis was used to identify that stage or factor in the life cycle that explained the largest amount of the total variation in population size. Of 16 species considered, the single most important factor in 8 species (including *Colias alexandra*; Hayes, 1981) was the failure to lay the full complement of eggs. That is, in 50% of the cases studied, variation in realized fecundity was the single most important determinant of population fluctuations.

It appears, then, that the population dynamics of butterflies may be intimately connected with thermoregulation. I propose that the connec-

tion of weather to population ecology is mediated by thermoregulation and flight in relation to realized fecundity. This proposal both highlights the important role of thermoregulation in butterfly ecology, and provides us with a mechanistic way of studying the effects of weather variation on population dynamics in insects.

In summary, the flight space is a useful tool in summarizing the ranges of weather conditions in which a particular butterfly group can achieve the body temperatures needed for flight. Empirical and modeling approaches have been used to show differences in flight spaces among species, and to identify the morphological and behavioral determinants of these differences. The small body size of butterflies makes them particularly susceptible to short-term weather variation, and it has been shown that overheating resulting from such variation can affect survivorship, fecundity, and territorial defense. Weather conditions that prevent active flight may increase predation on roosting butterflies. More generally, weather limitations on the time available for flight activity may reduce the realized fecundity in many butterflies by limiting the time needed for oviposition. Recent demographic evidence shows that variation in realized fecundity is the single most important factor in fluctuations in population size in many cases. This suggests that weather and thermoregulation may be an important determinant of butterfly population dynamics, through their effects on flight time and oviposition.

Conclusions: Our Current State of Knowledge and Ignorance

1. Physiological mechanisms of thermoregulation are not of general importance for butterflies. Instead, they rely on behavioral mechanisms, in particular on regulation of heat gain by orientation and posture relative to the sun. The behavioral, morphological, and physical determinants of radiation absorption have been studied in some detail; as a result, we now have a quantitative understanding of the principal mechanisms of heat transfer in all of the major basking postures except body basking. On the other hand, the relation of convective heat loss to behavioral orientation to wind has been examined in only two groups, with conflicting results, and its importance for butterfly thermoregulation remains unknown.

2. Surveys of basking posture have been done for many temperate American groups, but we know little of the relative advantages of these postures in different groups, and careful comparative studies within related groups are essential. Basking posture appears to be correlated with both phylogenetic relationship at the family level and body size, but the generality and causal bases for these correlations are unknown. The importance of thermoregulation in tropical butterflies is almost entirely unexplored.

3. Wing color, in particular wing melanization, is an important component of thermoregulation in a number of butterfly groups through its

effects on radiation absorption. In most butterflies, color only at the bases of the wings are relevant to thermoregulation; and color, not pattern, at the wing bases is the key characteristic. One notable exception is for pierine butterflies that use their wings as solar reflecting devices, for which the entire dorsal wing pattern may be relevant to thermoregulation. These studies on the thermal significance of wing color suggest that a detailed understanding of the physical and behavioral mechanisms involved is essential.

4. The flight space is a useful tool in summarizing the ranges of weather conditions in which flight can occur, and has been evaluated empirically and theoretically for a number of butterfly groups. However, the morphological and behavioral characteristics determining the flight space have only been evaluated for one genus.

5. The small body size of butterflies makes them particularly susceptible to weather variation on a time scale of one to a few minutes. In a few well-studied groups, such short-term variation has been shown to affect survivorship, fecundity, flight, and territorial defense.

6. Several lines of evidence suggest that weather-related limitations on the time available for flight activity may reduce realized fecundity by limiting the realized oviposition rate in many temperate butterflies that lay eggs singly. Demographic studies indicate that variation in realized fecundity due to weather variation is a major determinant in population fluctuations in temperate butterflies. Thus, thermoregulation and flight, through their effects on realized fecundity, may be a vital link connecting weather to the population dynamics of many butterflies. A comprehensive experimental demonstration of this system of links, and its general importance for butterflies, is still lacking.

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Protein and Lipid Composition of *Colias philodice* and *C. eurytheme* Spermatophores and Their Changes Over Time (Pieridae)

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Abstract. During copulation male *Colias philodice* and *C. eurytheme* accessory gland secretions fill the appendix bursa and form a spermatophore in the female's bursa copulatrix. These secretions represent 6-7 percent of male body mass. Protein represents 10 and 23 percent of the dry mass of spermatophores and appendix bursa contents respectively. Total lipid in spermatophores was nearly equal to protein content. Hydrocarbons, nonhydrocarbons, and phospholipids represent 47, 41, and 12 percent, respectively, of total lipid. Hydrocarbons were composed of 25 components ranging from 19 to 38 carbon atoms. Ninety-three percent of total hydrocarbons were n-alkanes. Nearly equal amounts of cholesterol, diacylglycerols, triacylglycerols, and free fatty acids accounted for the nonhydrocarbon fraction.

Proteins and hydrocarbons leave the spermatophore, either intact or following degradation, more rapidly than the nonhydrocarbon and phospholipid fractions which stay within the spermatophore until the spermatophore is almost completely deflated.

Since other studies have demonstrated transfer of protein from male to female, and its subsequent use in egg production, the implications of presence of lipids in spermatophores are discussed.

Introduction

In many insects, a spermatophore is passed during copulation. The non-sperm portion of the spermatophore is composed of male accessory gland secretions that are absorbed by the female and possibly used for maintenance or egg production (Thornhill, 1976; Friedel & Gillott, 1977; Boggs & Gilbert, 1979; Boggs, 1981; Boggs & Watt, 1981). Oviposition is stimulated by these accessory secretions in Orthoptera (Pickford, et al., 1969; Friedel & Gillott, 1976), Diptera (Riemann & Thorson, 1969), and Lepidoptera (Benz, 1969; Yamaoka & Hirao, 1976). The possibility that males may affect the rate of oviposition as well as contribute nutrients for egg production has implications concerning the structure and evolution of insect mating systems.

Most investigations of spermatophore utilization have focused on the use of amino acids (Goss, 1977; Boggs & Gilbert, 1979; Boggs, 1981; Boggs

& Watt, 1981) or protein (Friedel & Gillott, 1977) by the female. To date, however, only Gerber et al. (1971) have presented data on the biochemical composition of spermatophores and the absorption of nonprotein components by the female. Their histochemical study of a meloid beetle spermatophore indicated presence of polysaccharides, proteins, phospholipids, and neutral lipids. In this study the spermatophore composition of *Colias philodice* and *C. eurytheme* spermatophores and temporal changes in their composition are described. In addition, a preliminary analysis of the contents of the appendix bursa, an organ associated with the bursa copulatrix (the receptacle for the spermatophore) (Figure 1), is presented.

Materials and Methods

Collection and Dissection of Butterflies

Colias philodice and *C. eurytheme* females were collected from May to October, 1979, in alfalfa fields at the Arizona State University Field Laboratory, Tempe, Arizona. From 28 August to 5 September 1979 *C. philodice* and *C. eurytheme* were sufficiently abundant to allow field collection of mating pairs. Copulating pairs were collected and transported in small vials to the laboratory within two hours of capture. The two species produce viable hybrids (Grula & Taylor, 1980a) and so are treated as one group here.

All spermatophores and appendix bursae were removed from females by dissection under water just prior to analysis. The duct between the bursa copulatrix and the appendix bursa was ligated with 6/0 silk. The appendix bursa was then separated from the bursa copulatrix (which contained the spermatophore) and both organs were placed in glass vials.

Spermatophores and appendix bursae from free flying, field collected females were divided into three classes using a qualitative technique
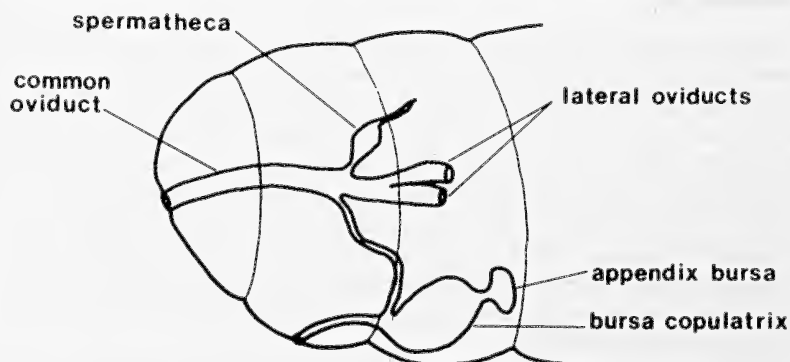

Fig. 1. Diagramatic view of the Lepidopteran female reproductive tract.

based on variation in size and shape of the structures and representing changes with time since deposition (Rutowski, 1981). These classes are: condition 1 — round and full; condition 2 — partially deflated; and condition 3 — almost completely deflated. Spermatophores and appendix bursae from field collected mating pairs are classified as newly mated (NM). These spermatophores are visually similar to condition 1 spermatophores.

Wet and Dry Mass

Single spermatophores and appendix bursae were placed in tared vials and wet mass determined to 0.01 mg. Samples were dried to a constant mass at 80°C.

Protein Analysis

Protein contents of both spermatophores and appendix bursae were analyzed using the BioRad method (Bradford, 1976). This color-photometric technique enables quantification of protein but is insensitive to other forms of nitrogen. Single spermatophores were macerated and then digested for approximately 2 hr at room temperature in 2 ml in 1N NaOH. One tenth ml aliquots were transferred to sterile borosilicate culture tubes and 5 ml of diluted BioRad concentrate (5:1 with distilled water) added. Samples were mixed with a vortexer for 30 sec and allowed to react for a minimum of 5 min, after which the concentration of protein was estimated with a Bausch and Lomb Spectronic 20 at 595 nm using a bovine serum albumin standard curve. Three samples were analyzed for each spermatophore and the absorption values averaged.

Lipid Analysis

A. Extraction and Separation

Spermatophores were pooled by class (for pool sizes see Fig. 3) and allowed to stand for one hr in 5 ml of chloroform/methanol (2:1) at room temperature. The lipid extract was subjected to a complete Folch wash (Ways and Hanahan, 1964), evaporated to dryness under nitrogen, and weighed to 0.01 mg.

Total lipid samples were separated into three classes (hydrocarbons, nonhydrocarbons, and phospholipids) by silicic acid column chromatography (BioSil A) (Jackson, et. al., 1974). Following separation, each fraction was weighed to 0.01 mg.

B. Hydrocarbon Analysis

Argentation TLC, developed in hexane:diethyl ether:acetic acid (90:10:1 by volume), was used to check for unsaturation of the hydrocarbon fraction (Jackson, et al., 1974). The hydrocarbon fraction was analyzed by flame ionization detection gas chromatography using 183 x 0.32 cm glass columns packed with 3% OV — 101 on 100/120 Gas Chrom

Q; oven temperature was programmed for 220° to 300°C at 2°C/min. Peaks were identified by comparison to retention times of known standards and quantitated by electronic integration.

C. Nonhydrocarbon Analysis

Nonhydrocarbon fractions were analyzed by spotting a 1 ul sample on 250 um Silica Gel G plates (BioRad Laboratories) and developed in hexane:diethyl ether:formic acid (80:20:2 by volume) to separate major classes of polar lipids. Plates were charred and bands identified by comparison to known standards.

Results

Gravimetric Analysis of Male Imparted Secretions

Mean wet masses of newly implanted spermatophores and appendix bursae contents were 3.8 ± 1.9 mg and 0.88 ± 0.49 mg respectively, yielding a total mass transferred during mating of 4.7 mg (Fig. 1). Though these masses include the walls of the bursa copulatrix and appendix bursa it was found (by weighing both organs removed from virgin females) that the mass of the organs was negligible (less than 0.01 mg; $N = 10$). The mean body mass of field collected *C. philodice* and *C. eurytheme* males was 70.4 ± 15.4 mg ($N = 35$). Therefore, the mass of a new spermatophore plus appendix bursa contents represents 6-7 percent of a male's body mass.

Dry mass for newly implanted spermatophores and appendix bursa contents averaged 2.0 ± 1.1 and 0.35 ± 0.24 mg, respectively (Fig. 1). These masses declined significantly as spermatophore condition went from NM to 2 (Fig. 1) (Scheffe's test, $p < .05$).

Protein Analysis of Male Imparted Secretions

Spermatophore and appendix bursae contents from newly mated females contain 0.20 ± 0.12 and 0.088 ± 0.05 mg of protein, respectively (Fig. 2). As a percent of dry mass, this represents 10 percent from spermatophores and 23 percent from appendix bursae contents. Protein content in both spermatophores and appendix bursae declines as the organs deflate from condition 1 to 2 (Scheffe's test, $p < .05$) and nears zero in condition 3 appendix bursae (Fig. 2).

Lipid analysis of Male Imparted Secretions

A. Gravimetric Analysis

Total lipid contained in condition 1 spermatophores was 0.17 mg (Fig. 3), declining as spermatophore condition changed from condition 1 to 2 (Scheffe's test, $p < .05$) and then remained unchanged from condition 2 to condition 3 (Fig. 3). Separation of the total lipid fraction showed that hydrocarbon, nonhydrocarbon and phospholipid fractions represented, respectively, 47, 41, and 12 percent of the total lipid content of condition 1
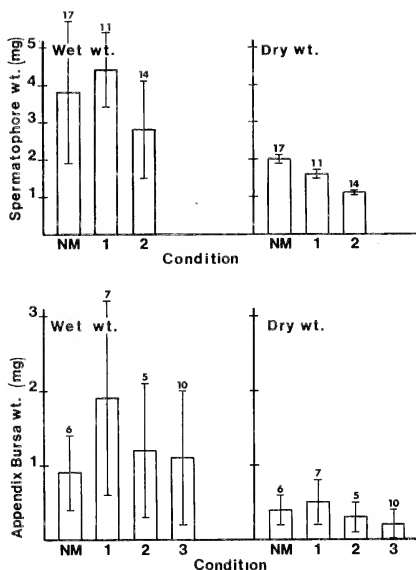
Fig. 2. Wet and dry masses of spermatophores and appendix bursae contents from *C. philodice* and *C. eurytheme* females. Numbers above each bar represent sample size. Brackets indicate one standard deviation. NM = newly mated. ND = no data available.
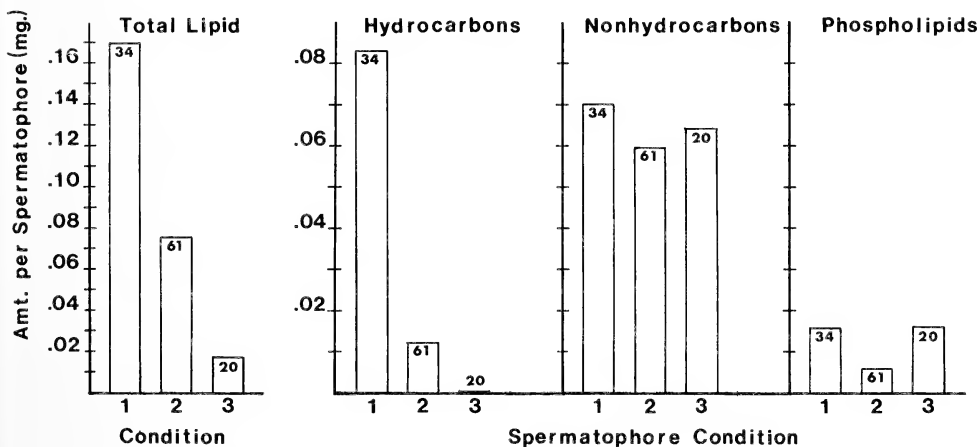

Fig. 3. The amount of protein per spermatophore (unhatched bars) and appendix bursae contents (hatched bars) from *C. philodice* and *C. eurytheme* females. Numbers above each bar represent sample size. Brackets indicate one standard deviation. NM = newly mated. ND = no data available.

spermatophores (Fig. 3). Only the hydrocarbon fraction declined as spermatophores deflated, while the weight of the nonhydrocarbon and phospholipid fractions remained constant (Fig. 3).

B. Hydrocarbon Analysis

Argentation TLC indicated that the hydrocarbons were completely saturated. Gas chromatographic analysis (GLC) of the total hydrocarbon fraction indicated the presence of over 25 components containing from 19 to 30 carbon atoms (Table 1). Normal alkanes represent 93 percent of the total hydrocarbon extracted, with chain lengths ranging between 25 and 29 accounting for 51 percent of the total (Table 1). There appear to be no significant differences in hydrocarbon composition between conditions 1 and 2 spermatophores. Due to lack of material, only one GLC separation was possible with condition 3 spermatophores and though no averaging of GLC data was possible, this single trace indicates no compositional differences between condition 3 and conditions 1 and 2 spermatophores.

C. Nonhydrocarbon Analysis

Visual analysis of charred TLC plates of the nonhydrocarbon fraction indicates that this fraction of spermatophore lipid contains sterols, diglycerides, triglycerides, and free fatty acids in nearly equal amounts with traces of alcohols and sterol esters as well. Because recoverable amounts were small, no attempt was made to quantify these components. While such visual analysis is admittedly crude, it indicates no change in composition of this fraction as spermatophores deflate from condition 1 to condition 3.

Discussion

During copulation a male *Colias philodice* and *C. eurytheme* fills the female's appendix bursa with a white, protein-rich substance and constructs within the bursa copulatrix a spermatophore containing both proteins and lipids. This deposition represents approximately 6 to 7 percent of the male's body mass.

There are two ways male butterflies could increase the number of offspring produced per mating by supplying material via a spermatophore. Males could supply chemicals that increase the rate of egg production, or males could supply nutrients that decrease the time required by females for foraging, and thus increase available oviposition time. This study indicates that male *C. philodice* and *C. eurytheme* supply materials that could operate in both ways.

Protein Content of Male Imparted Secretions

Protein is an important component of spermatophores representing approximately 10 and 23 percent, respectively, of spermatophore and appendix bursa dry masses, and 12 percent of total male secretion. Pro-

Table 1. Identification and percentage composition of hydrocarbons from condition 1 and condition 2 spermatophores of *Colias philodice* and *C. eurytheme* butterflies.

GLC Peak No.	ECL	Condition 1	Condition 2	Alkane
			Percentage Composition	
19	19	trace*	1.7	n-Nonadecane
19-B	19.6	—	trace	unknown
20	20	trace	.8	n-Eicosane
21	21	1.6	1.7	n-Heneicosane
22	22	3.6	2.6	n-Docosane
23	23	6.4	5.2	n-Tricosane
24	24	8.1	6.5	n-Tetracosane
25	25	10.1	8.6	n-Pentacosane
26	26	9.7	8.6	n-Hexacosane
26-B	26.6	trace	trace	unknown
27	27	10.0	9.2	n-Heptacosane
27-B	27.6	trace	—	unknown
28	28	12.8	12.8	n-Octacosane
28-B	28.4	—	.7	unknown
29	29	9.1	9.5	n-Nonacosane
30	30	5.5	6.4	n-Triacontane
30-B	30.6	—	.6	unknown
31	31	5.5	5.9	n-Hentriacontane
32	32	3.1	3.6	n-Dotriacontane
33	33	1.5	2.6	n-Tritriacontane
34	34	1.6	1.0	n-Tritetracontane
35	35	1.6	1.0	n-Tripentacontane
35-B	35.2	1.1	.7	unknown
36	36	1.1	trace	n-Trihexacontane
36-A	36.2	trace	—	unknown
36-B	36.6	.8	1.3	unknown
37	37	trace	—	n-Triheptacontane
38	38	2.1	1.6	n-Triheptacontane
		95.2	92.2	

* less than 0.5%
ECL = equivalent chain lengths

teins are important constituents of insect eggs (Clayton & Edwards, 1961) and, while some protein components (amino acids) are available to adult butterflies from dietary sources (Baker & Baker, 1973), males, by supplying protein or its components could increase time available for oviposition by decreasing the amount of time required by the female for foraging.

Rutowski (1978) has shown time to be important to ovipositing female in
C. philodice and *C. eurytheme*.

Lipid Content of Male Imparted Secretions

Total lipid recovered from spermatophores represents approximately 9
percent of dry mass, about the same amount as recovered spermatophore
protein (10 percent). The lipid fraction is composed of nearly equal frac-
tions of hydrocarbons and nonhydrocarbons (cholesterol, diglycerides,
triglycerides, and free fatty acids) and small amounts of phospholipids.

The hydrocarbon fraction, either intact or following degradation, leaves
the spermatophore while other fractions persist. Hydrocarbons are used
as waterproofing agents by many insects (see Jackson & Baker, 1970 for
review) and may be used by female insects to waterproof eggs, being
incorporated during chorionation. Synthesis of hydrocarbons by insects is
mediated by ecdysone (Arnold & Regnier, 1975), which is at low levels at
eclosion (Riddiford & Truman, 1978). Since copulation immediately
follows female eclosion males may allow females to oviposit sooner by
supplying hydrocarbons. It is interesting to note that 51 percent of the
hydrocarbon fraction is of C_{25}-C_{29} chainlengths. The male pheromone
(received by the female during courtship) contains C_{23}, C_{25}, C_{27} and C_{29}
hydrocarbons (Grula & Taylor, 1980b). By assessing male pheromone
production during courtship females may be able to determine a courting
male's ability to produce a spermatophore. This could explain Rutowski's
observation (1979) that previously mated males were much less persis-
tent in courtship.

The nonhydrocarbon fraction consists of approximately equal amounts
of sterols, diglycerides, triglycerides and free fatty acids. These com-
ponents are the major nonhydrocarbon components found in insect eggs
(Svoboda, et al., 1966). It is reasonable to suggest that male nutrient
investments of this nature may substantially decrease the time required
for female foraging. Further, since sterols cannot be synthesized by
insects (Clayton & Edwards, 1961) availability of this nutrient may directly
limit egg production.

It is obvious from the discussion above that many questions remain
unanswered about spermatophores and their functions as paternal
investment. It is clear however, that spermatophores can no longer be
viewed as just sperm or a single resource. Spermatophores are a complex
of chemicals, any or all of which could potentially increase the number of
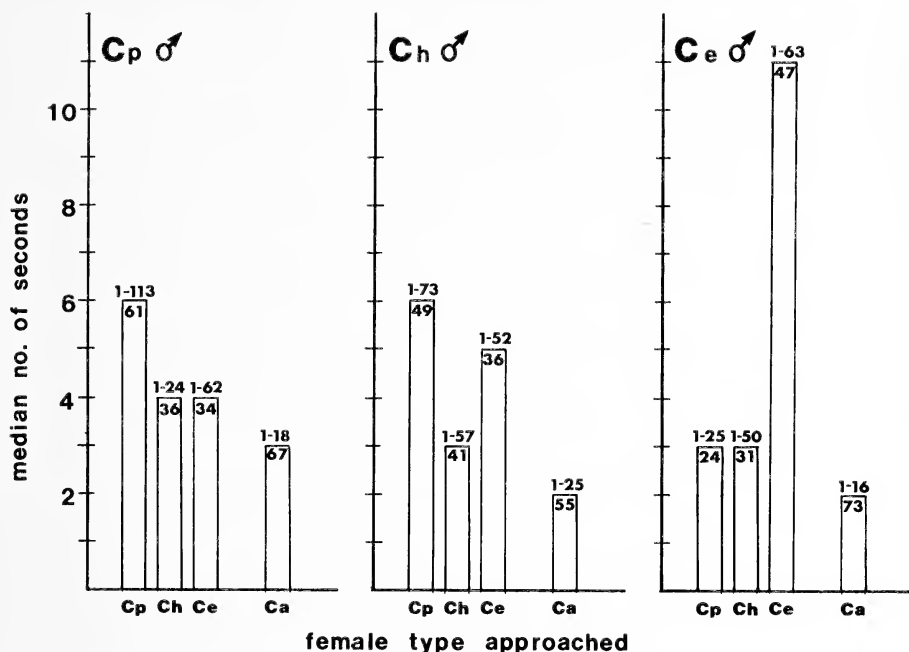offspring resulting from a mating.

Fig. 4. Total lipid and the 3 major classes of lipids extracted from spermato-
phores of *C. philodice* and *C. eurytheme*. Numbers within each bar rep-
resent the number of spermatophores within each pool.

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A Butterfly-Moth (Lepidoptera Castniidae) from the Oligocene Shales of Florissant, Colorado

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Abstract. An Oligocene fossil from Florissant, of the moth family Castniidae is named as *Dominickus castnioides*. The find may be of particular interest because indications are that the Castniidae seem to represent an early branch from the same stem which led to the present day Rhopalocera or butterflies.

Introduction

The Florissant Lake Bed Shales outcrop around the hamlet of Florissant in Teller County, Colorado (105° 19′ W. Long. x 38° 56′ N. Lat.). They have attracted attention from several generations of entomologists since their discovery as insect-bearing beds in the 1870's, by A. C. Peale M.D., a geologist on the Hayden Survey of the Territories.

The shales are composed of fine to coarse pyroclastic particles from Oligocene volcanics present near Guffey, some ten miles (16 km) to the southwest. Thousands of insect fossils have been recovered from these shales, and in the course of time more than one discovery has been made of the wing impressions of Lepidoptera, but these have been rare as compared with indications of the remains of other fossil insects.

While a member of the staff of the University of Colorado in Boulder, some years ago, I made several visits to Florissant but, despite some twenty hours spent in splitting these shales at a favorable locality, failed to find any trace of a lepidopteran fossil, although remains of other insect orders were obtained for the University collection.

F. Martin Brown recently sent me a lepidopteran wing specimen from these shales, for study. It was from a small collection of the fossils preserved in the Field Museum of Natural History in Chicago, where it is registered as their no. P.22949.

At first sight the wing impression appeared very confusing, but after detailed examination, making independent drawings at intervals of time and using different lightings, it became evident, as had been detected earlier by Brown, that the insect had died with its wings folded down over its body in such a fashion that the apices of the two forewings had chanced to be so exactly superimposed that the venation of one forewing was imprinted on the other with no more than a fractional lack of register. Thus there was formed a 'ghostly' repeat of the vein pattern of the right forewing below, on the left one, exposed above. No trace of the body sur-

vived and the hindwings were gone, save for a faint probable impression of a frenulum, as will be mentioned in a later paragraph of this paper.

Two photographs of the Oligocene fossil are shown, the best of more than a dozen taken using different artificial lightings, on ektachrome film. Figure 1 was taken at natural size and is now enlarged. White light was directed, at close to 45° angle, using also general illumination from a fluorescent tube light with added black light. This chanced to reveal a rather clear indication of the main lines of the venation and, so far as preserved, an indication of the outline of the wing itself; the impressions interpreted as those of the underlying right wing venation are sufficiently differentiated as to give some confidence that they may be distinguished from the veins of the overlying and more useful left wing.

Figure 2 was taken at twice natural size using only white light, the lamp source being set at about 30°, again from the upper right. This photograph does not emphasize so clearly the full outline of the wing, but it has given excellent indication of the veins of the left wing with relatively little interference from the underlying veins of the right wing.

In both of the above described photographs there is a suggestion of a differentiated or darkened apical area of the wing. It is not clear to me whether the difference registers an indication of a former wing color pattern or whether it is an artifact of chance.

Figure 3 is a drawing showing a deciphering of as much of the venation as preserved on the upper side of the left forewing. It has been mirror-imaged to conform to a convention of depicting the right wing when making comparisons with other species. The veins are labelled according to the system used by me in my earlier work, based on the notations of R. J. Tillyard, save that the postcubital vein is indicated as Pcu and the following, anally situated veins are indicated as vannal veins, 1V and 2V, following the lead of Snodgrass (1935), and supported by Ehrlich (1958).

Family Position of the Oligocene Wing

An early conclusion was reached that there was no good evidence linking the fossil with any member of the homoneurous Lepidoptera. Factors considered included the wide wing and the rather midwing position of the fork of Cu_{1a} and Cu_{1b}. This led indirectly to a consideration whether it could be linked with a hypothetical ancestor of the Hesperioidea and the Papilionoidea. It then became evident that there was a distinct indication of a possible relationship with the still living and curious day-flying moths of the family Castniidae, often known as Butterfly-moths.

In the superfamily Castnioidea there are known to be more than two hundred living species, usually recognized as divided among three families, of which the Castniidae occur chiefly in Australia, and South and Central America. Members of the other two families live in South East Asia, Madagascar and continental Africa.
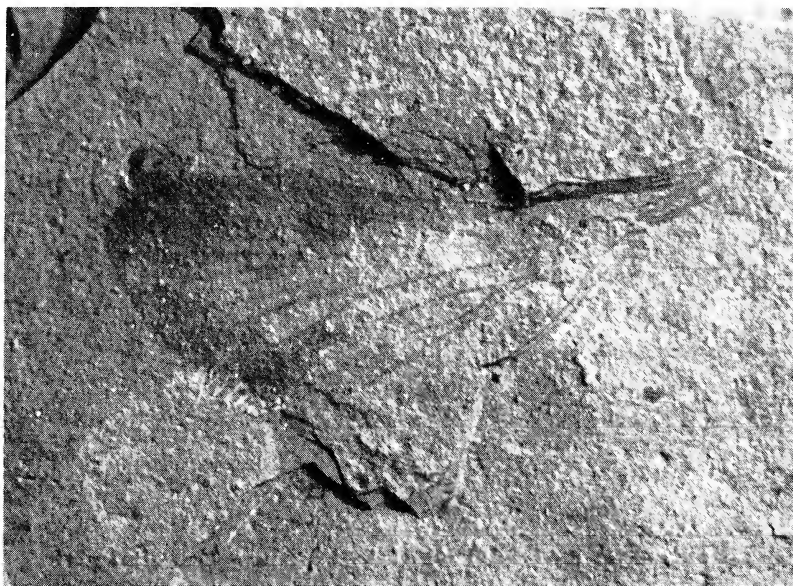
Fig. 1. *Dominickus castnioides*. Florissant, Oligocene. Forewing showing wing outline and faint impressions of a possible wing pattern.
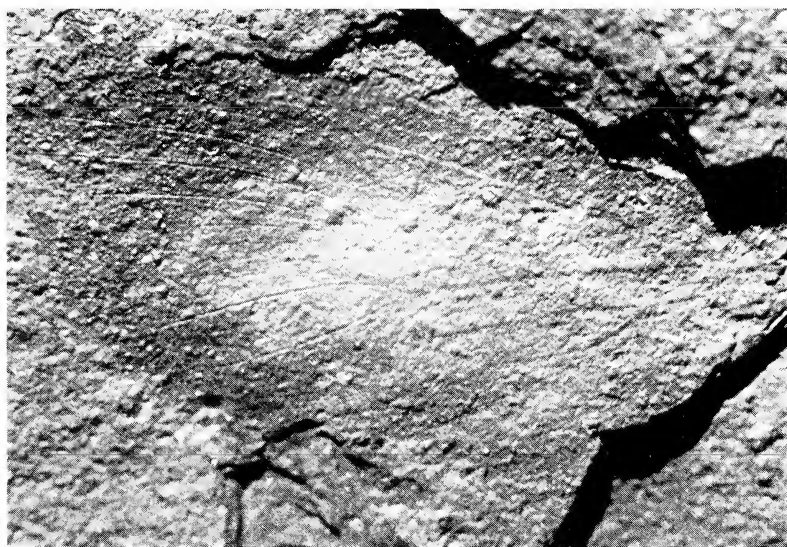

Fig. 2. *Dominickus castnioides*. Florissant, Oligocene. Forewing with low lighting to show principally the veins of the left wing.
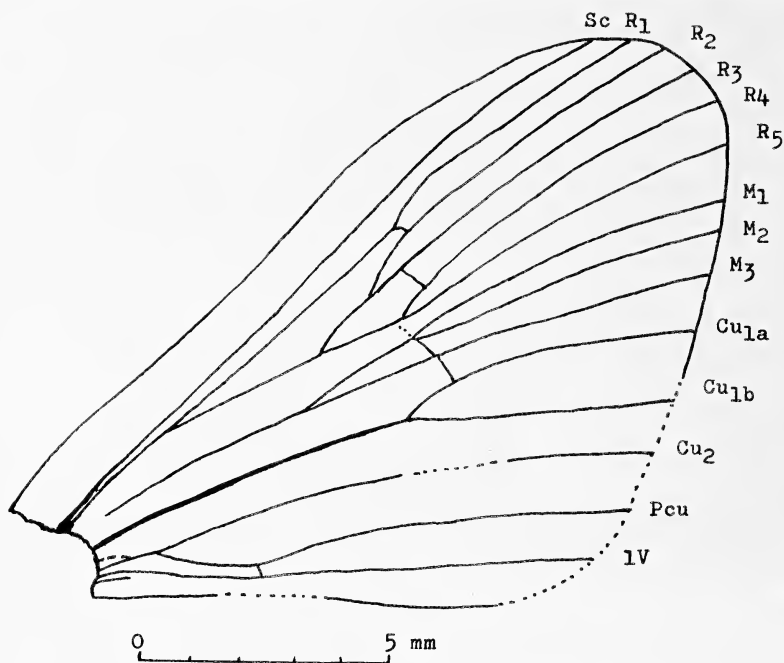
Fig. 3.   Venation of forewing of *Dominickus castnioides*, Florissant, Oligocene;
presumed to be of a male.

The genus *Synemon sensu latu*, with perhaps fifty species occurs in
Australia. They live chiefly in the more temperate and sometimes semi-
arid parts of the continent. Some of them are of the size of the Oligocene
fossil under consideration. American species of the Castniidae are, or
should be, placed in several genera but there is still much uncertainty as
to generic terminologies and many authors still retain them all under the
one generic designation *Castnia*.

Unlike the generality of moth species the castniids possess clubbed
antennae like the butterflies and are thought generally to be day-flying.
They are noted for displaying bright and conspicuous color patterns on
the undersides of their wings as well as on the upper surfaces. In this
regard they resemble the butterflies and especially in tropical America,
flying in bright sunshine, some of them take part in the Mullerian
mimicry complexes which are a feature of some butterfly species. In
recent papers (Tindale,1980, 1981) I advanced a belief that members of
the family Castniidae may have preserved venational similarities com-
mon to a joint ancestor with the butterfly stem, perhaps in the Mesozoic.
For this and other reasons the Florissant fossil may be of particular
interest and may be described in the following terms:

Family CASTNIIDAE

Dominickus Tindale, **new genus**

Description. Forewing broadly triangular, with rounded apex, and with rather straight termen, and almost straight hind margin. Venational pattern substantially of castniid type with R veins supporting the costal third of the wing. Sc vein is simple, R_1 from R_s at one-fifth, an ir crossvein linking R_1 with R_2 at three-fifths; R_3 and R_4 also joined by an ir vein after branching of R_4 and R_5, thus forming a cell. R and M_1 were almost certainly joined by a crossvein, rm, in the middle of the wing, but the presence of a coarser than usual particle has created a defect; in the drawing of the venation its likely position has been indicated by several dots. Cu_1 is a particularly strong vein in its basal half, branching to Cu_{1a} and Cu_{1b} close to the central point of the wing. Cu_2 and Pcu are joined near the base of the wing and Pcu is linked with 1V by a crossvein. There is a short indication of a possible 2V near the base of the wing.

Type. *Dominickus castnioides*. From the Oligocene Lake Bed Shales of Florissant in Teller County, Colorado.

The single species so far recognized in this genus appears to be a member of the superfamily Castnioidea and has been placed, on preliminary assessment of data, as belonging within the family Castniidae for reasons given in the general discussion which follows. The generic name is proposed in memory of Dr. Richard Dominick who did so much for the study of the moths of North America during his all too short life.

Dominickus castnioides Tindale, **new species**

Description. Its characteristics are as set out in the above generic description and shown in the accompanying drawing of the venation and the photographs. The state of preservation does not indicate the wing scales but the softened outline of the preserved part of the termen suggests a fringe similar to that present in other Castniid moths. Photographs seem to suggest the survival of indications of a color pattern in which the costal area narrowly from near the base and more widely from midwing was dark-colored as also the termen to the hind angle, with a broad band of some possibly lighter color extending from the costa at two-thirds toward the hind margin as far as M_3 where it terminated. The basal part of the wing appears to have been light-colored, with the hue extending to the hind margin. The veins in the light-colored areas perhaps were marked by darker scales than the rest of the wing.

The length of the preserved part of the wing, virtually its whole, is 16.4 mm and its width, measured from midcosta to the hind angle, is 9.4 mm.

Type. A forewing, no. P.22949 in the Field Museum, Chicago, Illinois. It was taken from the Florissant Lake Bed Shales, of Oligocene Age, in Florissant, Teller County, Colorado (105° 19′ West Long. x 38° 56′ North Lat.).

Relationship of *Dominickus castnioides*

Resemblances between this species and other members of the family Castniidae were noted first during a comparison with the venation of a Western Australian species of the genus *Synemon* identified as *S. leucospila* Meyrick 1891 and figured herein (Fig. 4). The drawing shows a ventral view of the forewing of a male. Its length, 16 mm, is close to that of the
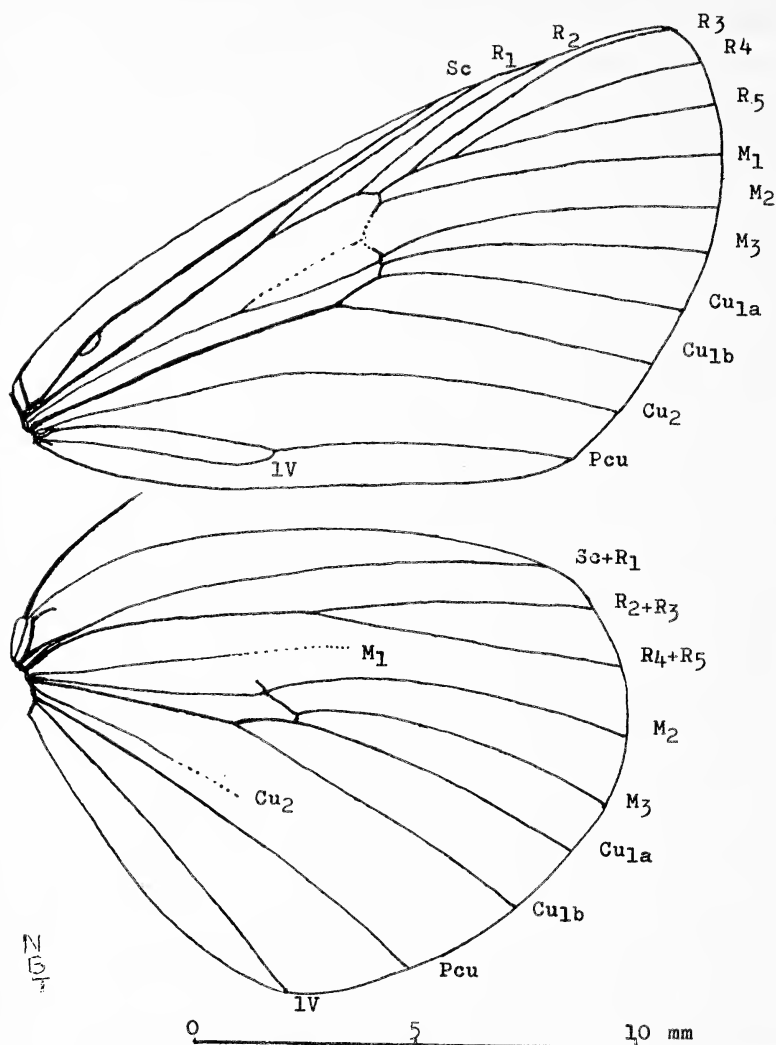
Fig. 4.   Venation of wings of a male of *Synemon leucospila* from Hawks Head
          Lookout, Murchison River, Western Australia.

Oligocene fossil under consideration. The hindwing also is shown to indi-
cate the length and general position of the frenulum. The depicted
specimen was one of a series taken flying in mid-afternoon at Hawks
Head Lookout, two miles (3.2 km) south of the mouth of the Murchison
River on 6 November 1968. There are distinct resemblances between *S.
leucospila* and the fossil, but the M_1 vein was less well developed, and 1V
did not extend to the margin in the living species. Through the kindness

of L. E. Pena G. of Santiago I was able to make comparison also with examples of a Chilean species identified as *Castnia psittacus* (Molina, 1781) by Ureta (1955) which, although larger in size showed an even closer resemblance to *Dominickus*, with close similarities in the M_1 region of the wing and both Pcu and 1V vein extending to the anal angle, with a well-developed 2V vein in the place of the remnant only visible in *S. leucospila*. The ventral view of the forewing venation of a male of this South American species is shown as Figure 5. Its length is 22 mm and it was taken at Divisidero, Ovalle, Chile, 15/17 December 1977 by L. E. Pena G.

Links between the Chilean species and the fossil from Florissant seem greater than with *Synemon*. Both M and Pcu areas are similar and the R veins, in the center of the wing show considerable resemblances and comparable complexities of linkage; the principal difference appearing to be the lack of an ir crossvein between R_1 and R_2 in *C. psittacus*, as also in other Castniids examined. This difference could encourage a view that *Dominickus* should be set in a family of its own but within the Castnioidea.

Near the base of the wing of the fossil there is a faintly appearing oblique mark which I had not noticed when first making observations. However F. Martin Brown, upon learning of my tentative identification linking the
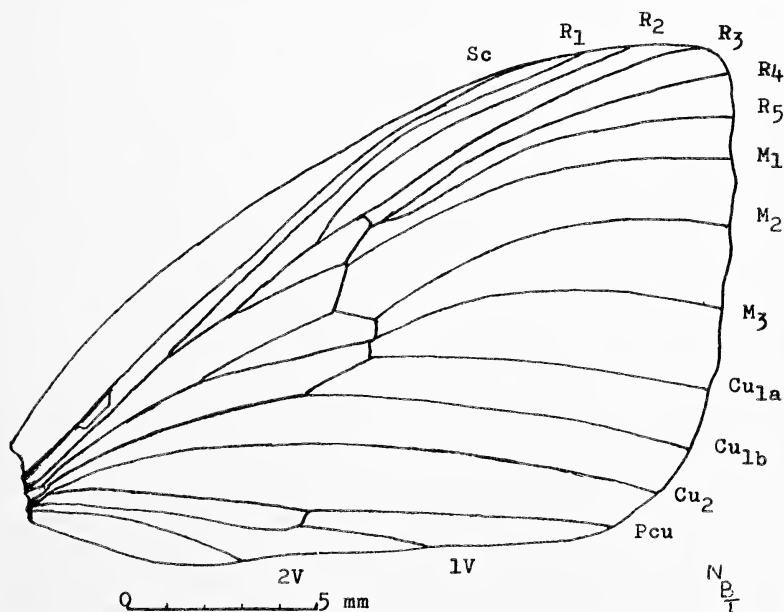

Fig. 5.   Venation of forewing of a male of *Castnia psittacus* from Divisidero, Ovalle, Chile.

fossil with the Castniidae, wrote 'I thought I saw a trace of frenulum near the base of one of the overlapping wings when I studied the fossil, but was not at all sure.' Such an obliquely set raised indication of pressure from beneath does appear at an appropriate place and also seems to have left traces where a frenulum-like spine passed under the M and Cu veins. if the interpretation is valid we may assume that the type specimen of *D. castnioides* could have been that of a male.

Superimpositions of drawings of the three venations mentioned above were studied. Using Cu_1 as a baseline and the point of parting of Cu_{1a} and Cu_{1b} as an arbitrary central point in the wings it appeared that the direction of change with time between *Dominickus* and the living *Synemon* showed a strengthening of the costal area by the contraction and crowding of the R veins. There is also considerable expansion of the terminal area of the wing in *Synemon*. When a similar comparison was made between the Oligocene fossil wing and the *Castnia* one from Chile the contraction and strengthening of the costal area was far less with time although the terminal expansion was similar to that in *Synemon*. From indications such as this we may be correct in assuming that *Castnia* as it occurs in America may be a little closer to *Dominickus* or has changed somewhat less than *Synemon*.

Having established a probability that the Florissant wing was linked with the American section of the family Castniidae a check indicated that while they were very numerous in the American tropics some species had ranges extending into more temperate areas and that no fewer than five species had been recorded from Mexico, two living less than 1250 miles (2000 km) south of Florissant, in Colorado. A short list of reported Mexican species included the following, with a few of their known localities:

Castnia atymnius Dolman	*VERA CRUZ: Cordoba (subspecies futilis* Walker)
Castnia chelone Hopffer	VERA CRUZ: Cordoba, Jalapa and Orizaba
Castnia escalantei Miller	GUERRERO: Acahuitzola
Castnia estherae Miller	MICHOACAN: Purua
Castnia inca Herrich-Schaeffer	TAMAULIPAS: Tampico

Not having immediate access to any of these it was fortunate that Miller (1976) had made drawings of the basal halves of the wing venations of several Mexican species of *Castnia* which seemed to show close resemblances as well as variations of veins which could well link with the corresponding veins in *Dominickus*. Taking the data Miller gives for the species *Castnia escalantei*, which she described as new, it can be seen that there are detailed similarities in the Pcu and 1V veins although there is seemingly a difference in the absence in her drawing of one of the R veins, perhaps a casual difference, for in the species *Castnia estherae* which she also described as new the full complement of veins are present with the

complex arrangement of cells similar to *Dominickus*. The most outstanding difference seems to be the presence in *Dominickus* of what has been mentioned earlier in this paper as an apparent ir vein joining R_1 and R_2. The full significance of this ir vein is yet to be determined.

In other papers, Tindale, 1980, 1981 I have considered the possibility that members of the family Castniidae may supply indications of the ancestral line of the Papilionoidea and the Hesperioidea and therefore, if the evidence afforded by *Dominickus* is valid it can be assumed that the castnioid wing pattern was already well defined by the Oligocene. Further study of the Mexican species will very likely confirm what has been suspected by me for some time that the patterns of Lepidoptera evolution in subtropical North America were very ancient, as has been indicated by the even longer and most striking link evident between the Papilionid fossil *Praepapilio colorado* Durden and Rose 1978, from the Middle Eocene of the Green River Shales in Rio Blanco County, Colorado, and the living Mexican Papilionid *Baronia brevicornis* Salvin 1893.

C. (Xanthocastnia) viryi (Boisduval)	OAXACA, CHIAPAS
C. (Cyanostola) diva Butler	VERA CRUZ, CHIAPAS
C. (Orthia) delecta Schaus	VERA CRUZ
C. (Orthia) hectiae Dyar	VERA CRUZ
C. (Orthia) miustagma Dyar	GUERRERO

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Evidence for Host Plant Preferences in *Heliconius erato phyllis* from Southern Brazil (Nymphalidae)

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Abstract. The oviposition behaviour of female *Heliconius erato phyllis* was investigated in relation to 9 species of host plants belonging to the genus *Passiflora*. Larvae were reared on the same host plants to assess their viabilities, rate of development from eggs to pupae and pupal weights. Results indicate that the subspecies *phyllis* is oligophagic with an incipient specialization on *Passiflora misera*. Some results imply that plant abundance does not play a primary role in this specialization.

Introduction

Since Ehrlich and Raven's (1964) original article, the literature on coevolution of butterflies and plants has increased substantially. Among the most intensely studied groups of butterflies, are the Pieridae (see for instance Chew, 1977), Papilionidae (Rauscher, 1980; Rauscher and Papaj, 1983; Berenbaum and Feeny, 1981, among others) and Nymphalidae, particularly the tribe Heliconiini (a comprehensive treatment can be found in Benson, Brown and Gilbert, 1975). Few of these studies, however, investigate how coevolution between butterflies and plants originates; although relevant in this context is the work of Smiley (1978a, b) with three species of *Heliconius* from Costa Rica, where the primary determinants of monophagy were tested, the ecological factors predation and plant abundance as well as host palatability. This investigation contributes with additional data testing larval development parameters for the butterfly *Heliconius erato phyllis* on nine species of *Passiflora*. A brief consideration of adaptive strategies involved is also presented.

Materials and Methods

Adult *Heliconius erato phyllis* butterflies used in this study are from Rio Grande do Sul, the southernmost state of Brazil with both subtropical and temperate climate. This species is widespread, the populations exhibiting marked oscillations through the year, and local extinctions have been recorded (Saalfeld and Araújo, 1981; Pansera and Araújo, 1983). Sixteen females were used in oviposition tests, 12 from the wild and 4 from insectary matings. The species of *Passiflora* tested

were: *P. misera, capsularis* and *suberosa* belonging to the subgenus *Plectostemma; coerulea, elegans, alata, tenuifila, edulis* and *actinia*, subgenus *Granadilla*. These are 9 of the 13 available species in Rio Grande do Sul (Sacco, 1962, 1980) and include all those frequently used by *H. erato phyllis* in nature.

The experimental procedure followed two steps: in the first, females were isolated from passion-flowers for 48 or 96 hours. They then were offered pots with fresh plants on which to oviposit, one *Passiflora* species at a time. Because the results for the two isolation intervals were not significantly different, they were combined. Each test lasted 30 minutes, the female having 2 or 3 pots of the same species to oviposit. All the oviposition behaviour was carefully observed and the host acceptability ratio (H.A.) measured as the No. of tests with oviposition/No. of tests with foretarsal drumming behaviour. In order to quantify the preference for each host plant we calculated an oviposition rate (O.R.) as the No. of eggs/No. of tests with oviposition.

The second step involved feeding caterpillars until pupation on a single species of host plant. Eggs collected in nature or in the insectary were removed from the plant, weighed and placed individually in plastic vials in a controlled temperature chamber at 25°C. Larval growth was measured following the procedures of Smiley (1978b). For statistical analysis the data were transformed in natural logarithms.

Results and Discussion

Table 1 shows the results for oviposition ratio and index of preference of *H. erato phyllis* on the nine species of *Passiflora*. Three groups of host plants can be roughly distinguished concerning H.A.: those with high values (*P. capsularis* and *misera*), those with moderate, about fifty percent oviposition (*P. alata, edulis, suberosa* and *coerulea*), and those with low values (*P. actinia, elegans* and *tenuifila*). Interesting to note is that if

Table 1.   Host acceptability (H.A.) and oviposition rate (O.R.) in nine species of *Passiflora*.

Passiflora		H.A. (%)	O.R.
capsularis	(20)	100	1.3
misera	(27)	90	2.5
alata	(13)	60	1.5
edulis	(17)	57	1.0
suberosa	(16)	50	1.7
coerulea	(17)	50	1.2
actinia	(20)	33	1.0
elegans	(12)	0	0
tenuifila	(10)	0	0

( ) = number of tests made

one looks at the O.R. for the same plants there is relatively poor correlation; for instance, it is greater for *P. misera*, followed by *suberosa* and *alata*, only then by *capsularis*. Observations suggest, however, that the results here reported are similar to oviposition in the field near Porto Alegre, Rio Grande do Sul; we have found, whenever *P. misera, coerulea* and *elegans* are present in the same area, that eggs are found almost only in the first species. In other areas where *P. coerulea* is replaced by *suberosa*, the proportion of eggs on the latter is found to increase. In the Northwest of the State, where *P. tenuifila* is abundant, one of us (AMA) found only one egg in that plant during almost four years of observations!

The proportion of eggs reaching adulthood (egg to adult viability), the development time from egg to pupa and larval growth rates are presented in Table 2 and Figure 1. *P. suberosa* showed the highest percentage of viable adults, followed by *P. misera* and *capsularis*. *P. tenuifila* and *alata* were lethal to feeding larvae, while on *P. edulis* only 13% of eggs became adults (interestingly these last two species release great amounts of HCN when macerated—K.S. Brown, Jr., pers. comm.). The next two columns in the table are correlated; *P. misera* seems to be the most nutritious among species tested, caterpillars fed with it pupate after an average of 12 days. The results obtained for *P. elegans* are surprising since its mean exceeded

Table 2. Viable adults, development egg-pupa (mean $\pm$ S.D., days) and larval growth rates (mean $\pm$ S.D.) for different species of *Passiflora*.

Passiflora	No. of eggs	Viable adults		Development egg-pupa	Larval growth rate
		n	%		
capsularis	19	14	73	16 $\pm$ 1.7	0.72 $\pm$ 0.10
misera	72	54	75	12 $\pm$ 1.0	1.02 $\pm$ 0.13
alata	39	0	0	0	0
edulis	15	2	13	18 $\pm$ 3.6	0.59 $\pm$ 0.14
suberosa	54	48	88	15 $\pm$ 2.5	0.81 $\pm$ 0.12
coerulea	5	3	60	24 $\pm$ 4.6	0.47 $\pm$ 0.10
elegans	62	26	41	14 $\pm$ 1.9	0.87 $\pm$ 0.08
tenuifila	37	0	0	0	0

Passiflora actinia was not tested due to shortage of plants available for feeding caterpillars.
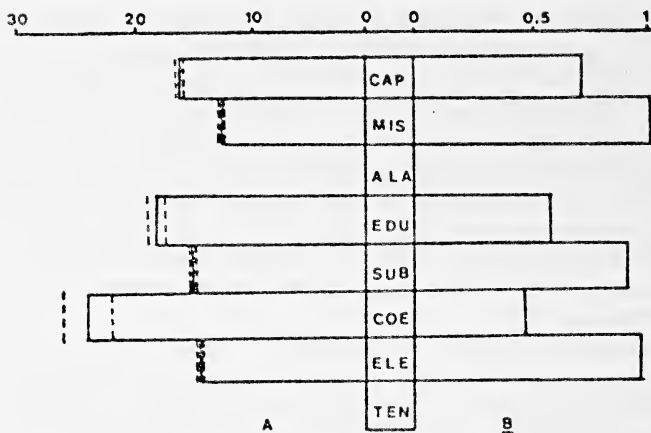
Fig. 1.   Graphical representation for development egg-pupa (A) (days), and larval growth rate (B). Hatched lines indicate standard errors. Species of *Passiflora*: CAP = *capsularis*; MIS = *misera*; ALA = *alata*; EDU = *edulis*; SUB = *suberosa*; COE = *coerulea*; ELE = *elegans*; TEN = *tenuifila*.

only two days that for *P. misera*. Considering that *P. elegans* is very common in some localities, collocated with *P. misera*, but is rarely used, we might conjecture that here there is an indication of palatability (or digestive efficiency) being precedent to an ecological factor (plant abundance). The same can be said of the *P. misera* and *suberosa* comparison. At Itapuã, near Porto Alegre, both species are equally common (Saalfeld and Araújo, 1981); nevertheless, eggs are found more frequently on *P. misera*. Another suggestion of palatability being precedent is the fact that *P. capsularis* and *tenuifila*, occurring abundantly at the Parque do Turvo show a remarkable difference in oviposition, that is, females prefer to lay eggs on *P. capsularis* instead of on *P. tenuifila* (this latter species was lethal in our experiment).

An analysis of variance carried out to test the equality of mean number of days for development from egg to pupa, and the mean pupal weights obtained for caterpillars fed with *P. misera, capsularis, elegans* and *suberosa* are shown in Table 3 (untransformed values for the latter parameter were: *P. misera*, 357 ± 31 mg; *P. capsularis*, 254 ± 80 mg; *P. elegans*, 329 ± 52 mg; *P. suberosa*, 325 ± 45 mg). For both variables the F-test showed highly significant results. However, when a partition of the "sum of squares between" is made, complementary results are obtained. So, if the mean number of days for development egg to pupa is considered, the comparison *misera × elegans* showed a significant difference, while the other two comparisons did not. If, on the other hand, mean pupal weight is taken into account, the only significant difference is that between *sub-*

Table 3. Analysis of variance for differences in development egg-pupa (a) and pupal weight (b). Original data transformed in ln x.

	Source of variation	SS	DF	MS	F
(a)	Between	1.2423	3	0.4141	20.10 ***
	(mis x ele)	0.2905	1	0.2905	14.10 ***
	(ele x sub)	0.0651	1	0.0651	3.16 n. s.
	(sub x cap)	0.0298	1	0.0298	1.45 n.s.
	Within	2.8028	136	0.0206	
(b)	Between	0.5746	3	0.1915	7.85 ***
	(mis x ele)	0.0663	1	0.0663	2.72 n.s.
	(ele x sub)	0.0021	1	0.0021	0.09 n.s.
	(sub x cap)	0.2539	1	0.2539	10.40 ***
	Within	3.3216	136	0.0244	

*** = P <0.001
n.s. = non significant

erosa × *capsularis*. On the basis of such analysis one can make the following scheme, where species united by a bar have equal means:

Development egg to pupa (days)
    Numerical values **misera** < **elegans** < **suberosa** < **capsularis**

    Statistical tests

Pupal weight (mg)
    Numerical values **misera** > **elegans** > **suberosa** > **capsularis**

    Statistical tests

Conclusions

The results here reported allow the following conclusions to be made: 1. *Heliconius erato phyllis* from the Southern Brazil is an oligophagic species; moreover, the *Passiflora* host plants preferred belong to the subgenus *Plectostemma*, supporting the findings of Benson et al. (1975). It is interesting to note that another *H. erato* subspecies, *petiverana*, has developed an specialization already, being classified as monophagic (Smiley, 1978b). 2. Caterpillars fed with *Passiflora misera* had the fastest development time from egg to pupa, suggesting a certain amount of digestive specialization. Since *H. erato phyllis* has a wider distribution than

this plant we believe this specialization to be a recent phenomenon. 3. As some of the *Passiflora* in this study are as abundant as *P. misera* in the area sampled (particularly *P. suberosa* and *P. elegans*) it seems that plant abundance does not represent the primary factor for specialization. 4. For the two variables presumably related to fitness (rate of development from egg to pupa, and pupal weight) the results obtained when caterpillars are fed with *P. misera* indicate that, as far as speed of development is concerned, *H. erato phyllis* in Rio Grande do Sul can be viewed as an opportunistic species, since in a variable environment (sometimes unpredictable—Saalfeld and Araújo, 1981), the more rapid the adult stage is achieved, more chances for reproduction occur. Pupal weight does not seem to be influenced by larvae being reared with *P. misera, elegans* or *suberosa*.

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A Critical Review of "Systematische Untersuchungen am *Pieris napi-bryoniae*-Komplex (s.l.)" (Lepidoptera: Pieridae) by Ulf Eitschberger

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Abstract. An extensive publication claiming to contain a taxonomic revision of the *Pieris napi* species-group is reviewed and analyzed. The results of the publication are largely rejected, and the taxonomic and nomenclatorial status of some taxa named therein revised. First steps are taken to protect unchanged continued use of some well established species-group names. Although a large amount of data are presented in this work, and the effort is enthusiastic and superficially impressive, there is no cohesive view of what *Pieris napi* represents, nor is the data base of any practical value.

Introduction

Bibliographical reference to the publication discussed in this paper: Eitschberger, U., 1984. Systematische Untersuchungen am *Pieris napi-bryoniae*-Komplex (s.l.) - Herbipoliana 1(1983)(1):I-XXII, 1-504; (2):1-601. - DM 360.--, published in 1000 numbered copies.

Although taxonomic revisions are extremely valuable in describing the systematic diversity of the living world, in making the information accessible to the audience interested, such works are few and far between. This work is not only without value, it is irresponsible. Its tragedy lies in the great deal of unrefereed effort and the resources which were squandered. In the following we will describe the shortcomings to justify its rejection.

The work was published in two parts which appeared jointly. The publication date stated is 1983, by implication the 31st of December. Nonetheless, the book was not distributed until February 1984, which gives us reason to believe that this is also the true date of publication according to the International Code of Zoological Nomenclature (ICZN)

Article 21 and 22. In consulting the relevant copyright library (i.e.
Deutsche Bibliothek in Frankfort a.M.) we have been advised that the
publishers complied with their obligation on 13 August 1984.

Part 1 consists of foreword by E. Reissinger followed by the complete
text of the work. This consists of a general section of 26 pages dealing with
elementary accounts of the morphology, eggs, larvae, pupae, etc., of the
Pieris napi species-group, followed by all the species monographs. The
whole work is written in an easy-going, narrative style as small talk be-
tween butterfly collectors. Part 1 concludes with a partial bibliography of
Pieris napi species-group and an assortment of black-and-white portraits
of some students of the genus *Pieris*.

Part 2 consists solely of plates. It is introduced by a list of explanations,
corrections and apologies, which is strange considering the high price of
the publication. In order, there are some 100 plates of line drawings of
androconia and some 140 plates of line drawings of male genitalia and
their parts, poorly executed and numbered in handwriting. Twelve plates
are devoted to female genitalia, drawn to the same standards. Another 12
plates are photographs of male and female genitalia, all more or less out of
focus and dissected so badly that it is difficult to distinguish between
anatomical structures and debris of unremoved tissue. Further 15 plates
contain simple line drawings of "standardized" legs, pupae, etc. and 18
plates of good stereoscan photos of various anatomic structures of adults
and early stages. The main part of this volume is comprised of nearly 100
color plates illustrating adults; the last 11 plates are devoted to an assort-
ment depicting some eggs, larvae, biotopes and Professor Lorkovic.

At first glance the color plates of adults butterflies are impressive, on
closer scrutiny they are disappointing:
- The specimens are not figured to the same scale, with the upperside
normally figured at a different magnification than the underside of the
same specimen (cf. e.g. holotype of *Pieris napi carlosi*: pl. 401, figs. 29 and
30). This is admitted in a casual reference (cf. pt. 2, p. 3).
- In the preparation of plates, all antenae were removed and later crudely
drawn in. Such perfunctory work produced at least one amusing "lapsus
calami": plate 439, fig. 27 shows a specimen with three antennae of which
two are "artificial" and the remnant of the third is real.
- Some specimens appear to be fakes: the specimen referred to as both a
holotype (cf. pt. 2, p. 402) and a lectotype (cf. pt. 1, p. 109) designated by
Eitschberger, is said to be identical with the specimen figured by Verity
(1905-1911) on plate XXXII, fig. 4 of his "Rhopalocera palearctica". A
simple comparison of both illustrations reveals considerable discrepancy,
suggesting at the least unbelievable sloppiness.
- There is no indication whatsoever concerning the scale of magnification
of the illustrations on color plates 579-599.
It is, therefore, safe to conclude that the illustrations in their vast

majority serve no useful purpose.

The systematic part of the work is arranged in a most unconventional way for a taxonomic work. All species group taxa are arranged in groups according to their distribution area, within which they are classified to species and subspecies. This arrangement is confusing. Bearing in mind the impressive 504 pages of text, it is worth listing the proportional composition of the work:

- About 100 pages are devoted to simple lists of examined material, by collection, specimen, locality.
- About 50 pages are devoted to listing the microscope slides made and examined.
- About 50 pages are reproductions of original descriptions and previously published material.
- About 25 pages are reproductions of distribution maps published elsewhere by other authors.

All in all, some 225 pages contain information which was redundant.

With reference to the unusual title of the publication: "Systematic investigations of the *Pieris napi-bryoniae*-komplex (s.l.)", we wonder if the author is unaware that:

- There is a decisive difference between the terms "systematic investigations" and "investigations of the systematics"?
- The use of hyphen in zoological nomenclature is determined by Art. 32(c) of the ICZN and limited to a few special cases?
- What he calls "Komplex (s.l.)" is generally known as the *Pieris napi* species-group?
- The name of the nomenclatorially oldest species, i.e. *Pieris napi* is adequate to denote every species-group, and the inclusion of the name *bryoniae* is unnecessary and confusing?

What is hidden behind such a long and complicated title can be found in the summary (pt. 1, p. 471): The work is a taxonomic revision. Consequently, it must be judged as such, whereby it is necessary to check whether it fulfills at least some requirements of that specialized form of scientific communication.

Taxonomic revisions are scientific works presenting both new material and including all hitherto known material relevant to the topic, where necessary reevaluated and newly interpreted, including the application of new methodology. Although taxonomic revisions vary greatly in scope from basic (essentially a taxonomic synopsis) to monographic, revisions must include the following features:

- definition and taxonomic position of the group under revision,
- taxonomic history of the group,
- key (or equivalent identification aid) to all taxa recognized,
- original combinations of and bibliographical references to all treated

taxa stated,
- full synonymy of all taxa recognized,
- index to all names presented,
- rationalized redescription of all recognized taxa,
- diagnostic features of all recognized taxa, and
- statements presenting clearly and logically all reasons for the actions
taken therein.

A communication that fails to fulfill most of the above features is certain to fall short of fulfilling the chief aim of the revision: to make the taxonomic group accessible to all zoologists and biologists beyond the very narrow circle of specialists well acquainted with its taxa. This work fails to fulfill even one of these points.

Comments on Terminology and Methodology

One of the striking features of the book is the author's inadequate vocabulary characterized by the lack of even the most basic terms, their misinterpretation and misapplication. This is documented by his description of an androconium (cf. pt. 1, p. 20; here translated from German): "Androconia [sic] look like a short-legged fat-bellied man [sic] whose head and neck have ingrown transitionlessly together. The head is covered by hair-fringes that can differ in length from specimen to specimen within a single species." (Eitschberger's description continues, but the sample translated here is considered adequate for the purpose). Androconia have no hair (or what are here called "hair-fringes"), but terminate in minute points; the "head and neck ingrown transitionlessly together" is generally known as lamina, and so on. Further on, he rejects the established term "androconium of the primitive type" and replaces it with cumbersome double-word "Makro- oder Riesen-Androkonium" (cf. pt. 1, p. 22). As the reason for the change, the author states that he does not follow the conventional term because he does not like it. It also appears that such well known terms as phallus and phallobase are totally unfamiliar, as he uses (cf. pt. 1, p. 29) aedoeagus instead of phallus, prefers to utilize "Rohr" (i.e. tube) instead of aedoeagus, and "Aussackung" instead of phallobase.

In addition to the strange morphological terminology, there are misused and confused taxonomic terms, of which some of the more important must be discussed here because their understanding is essential to decipher many confused statements:
- Eitschberger does not appear to know that 'nomen nudum' applies to a name that, if published before 1931, fails to satisfy the conditions of Articles 12 and 16, or, if published after 1930, additionally fails to satisfy the provision of Article 13(a) of the ICZN.
- He is unaware of the meaning, if not the existence, of the terms 'avail-

able name', 'unavailable name', 'valid name', 'invalid name' and 'infrasubspecific name'; or that they are defined by the ICZN. In particular, he does not seem to realize, that a name, to become available, must satisfy the provisions of Chapter IV of the ICZN, and that infrasubspecific names are defined by Articles 1 and 45(d) of the ICZN.

- He applies the definitive term 'nomen nudum' at random and uses his own creation "indirect nomen nudum" (cf. pt. 1, p. 188) for names that he believes to be unavailable and/or infrasubspecific in a conventional meaning.

- He does not appear to understand the difference between a binomen (which indicates in the trinominal system of names a monotypic species) and a trinomen (which indicates a polytypic species, in particular its nominate subspecies, by the repetition of the species-name as the third component of the combination) and denotes both polytypic and monotypic species with trinominal combinations.

- He appears unaware that 'comb.n.' indicates that a species-group name is being transferred to a genus different from that included in the original combination; that 'stat.n.' indicates a change of rank within the species-group is taking place, including a transfer of a subspecies-rank name to another species; that 'nom.n.' indicates that a new name is proposed to replace an existing name. Consequently, he uses the first two abbreviations at random as a meaningless appendix to some combinations, and the last abbreviation he places behind newly proposed infrasubspecific names.

- He lastly appears totally unfamiliar with the type-concept, in particular with the conditions regarding the designation and status of holotypes and lectotypes, and the purpose and conditions for the designation of neotypes. There is also an apparent unawareness that the loss of type(s) does not affect the nomenclatorial status of names.

Although the author refers frequently to the ICZN, which he calls "Nomenklaturregeln", and even volunteers advice to the International Commission on Zoological Nomenclature as to the treatment of what he calls "direct and indirect nomina nuda" (cf. pt. 1, p. 188), there appears to be a gap in understanding the Code. In no other way could this work have been produced.

A lack of general zoological knowledge is also apparent from repeated misspellings of commonly used terms, such as "Cariologie" instead of Karyologie, "Lectoparatypus" instead of Paralectotypus, "Heterozygote" instead of hybrid, etc.

The designation of figures as lectotypes, in disregard of Article 74(a)(ii) and 74(b) of the ICZN, must be mentioned (cf. comments on certain taxa treated in the work and pt. 1, p. 471: confusion between examined types and figures of types). Some insight into the approach to zoological

research is the fact that the author keeps type-material in his private collection instead of recognized depositories.

Valuable space in the publication is devoted to personal attacks on other students. One of the most severely attacked lepidopterists is the late B.C.S. Warren. The following example is characteristic, as well as amusing and amazing at the same time. Warren (1961) referred certain American populations to *Pieris bryoniae pseudobryoniae* Verity, although already aware of the unavailability of the name, because its original combination was *Pieris napi frigida pseudobryoniae* Verity, 1908 (Kudrna, 1983). The name *pseudobryoniae* had been widely used by various authors and raised to the rank of subspecies as *pseudobryoniae* auct. Warren's (1961) decision was taxonomically correct and justified because he was unable to establish unequivocally both the author and date of ssp. *pseudobryoniae* auct.—a task for the future reviser. Twenty years later, Eitschberger (1981) named a monotypic species *Pieris angelika angelika* [sic], denoted it by a trinomen but without a description, so that the name is a clear nomen nudum. In this publication, Warren (1961) is accused of misidentifying *Pieris angelika angelika* Eitschberger, 1981, calling it *pseudobryoniae* instead.

Eitschberger's approach to the study of *Pieris napi* species-group is in principle very simple, defining one purpose (cf. pt. 1, p. 2) to demonstrate that *Pieris napi* and *P. bryoniae* are two distinct species—but not to investigate their relationship. To achieve this goal, extensive use of selected data is effected, as evident by the treatment of the Fennoscandian taxa *napi, adalwinda* and *bicolorata*. Although fully aware of publications which have shown the close relationship between these taxa, including interbreeding both in nature and in the laboratory as well as morphological affinities (e.g. Peterson, 1949), he states that the latter two are subspecies of *bryoniae* (without stating the factual evidence to support such treatment). He substantially misinterprets statements made by other authors:

- For example it is claimed that Stephen & Cheldelin (1973) investigated 21 [sic] species of Hymenoptera [sic] and found no differences of Isoenzyme patterns, a statement to argue against the use of electrophoretic methods in taxonomy. In fact, Stephen & Cheldelin (1973) studied 21 *Bombus* spp. and four *Psythyrus* spp. clearly finding four distinctive patterns: three in *Bombus* spp. and one in *Psythyrus* spp.
- To further his argument against electrophoretic methods (cf. pt. 1, p. 35), he accuses Geiger (1981) of having concealed that deep-freezing of material can affect the results; in fact Geiger (1981:185) checked and discussed such effects.

Some essential publications on the genus, including Klots (1933) and Bernardi (1947) were omitted.

Comments on Newly erected Taxa and their Nomenclature

A remarkably high number of new taxa were created in this work: three new species, 21 new subspecies and 34 new infrasubspecific "seasonal forms". Two species-group taxa named earlier by the author (Eitschberger, 1981; Eitschberger & Hesselbarth, 1977) are also relevant to this discussion.

The names of infrasubspecific taxa were proposed "uninominally", but the original combination is unmistakeably implied from the specific or subspecific heading. Most of seasonal forms are not accompanied by any description or definition. Nevertheless, this is irrelevant because the names are unavailable according to the ICZN. We list the infrasubspecific taxa chronologically, with all original combinations reconstructed from implications given in the text. All monotypic species are listed here in binominal combinations regardless of Eitschberger's usual use of a trinomen; number in parenthesis following the name indicates the relevant page of original designation in part 1, where—contrary to the ICZN—these taxa are generally marked "nom.n."'

Pieris napi napi postnapae (p.43)
Pieris napi migueli antemigueli (p. 95)
Pieris napi santateresae antesantateresae (p. 99)
Pieris napi carlosi antecarlosi (p. 104)
Pieris napi lusitanica antelusitanica (p.105)
Pieris napi britannica postbritannica (p. 109)
Pieris napi meridionalis antemeridionalis (p.114)
Pieris napi muchei postmuchei (p. 135)
Pieris bryoniae flavescens anteflavescens (p. 151)
Pieris bryoniae wolfsbergeri postwolfsbergeri (p. 156)
Pieris bryoniae lorkovici postlorkovici (p. 161)
Pieris bryoniae marani postmarani (p. 170)
Pieris bryoniae vihorlatensis postvihorlatensis (p. 173)
Pieris bryoniae carpathensis postcarpathensis (p. 174)
Pieris bryoniae bicolorata postbicolorata (p. 179)
Pieris pseudorapae pseudorapae postpseudorapae (p. 187)
Pieris pseudorapae suffusa postsuffusa (p. 191)
Pieris pseudorapae balcana postbalcana (p. 202)
Pieris persis antepersis (p. 215)
Pieris dulcinea pseudonapi antepseudonapi (p. 241)
Pieris dulcinea saghalensis antesaghalensis (p. 246)
Pieris oleracea oleracea postoleracea (p. 263)
Pieris marginalis reicheli postreicheli (p. 301)
Pieris marginalis pallidissima antepallidissima (p. 306)
Pieris marginalis macdunnoughi postmacdunnoughi (p. 309)
Pieris marginalis mogollon postmogollon (p. 314)
Pieris marginalis guppyi postguppyi (p. 324)

Pieris acadica anteacadica (p. 336)
Pieris erutae reissingeri antereissingeri (p. 374)
Pieris erutae latouchei postlatouchei (p. 376)
Pieris erutae kneitzi antekneitzi (p. 378)
Pieris steinigeri antesteinigeri (p. 382)
Pieris extensa bhutya antebhutya (p. 387)
Pieris melaina postmelaina (p. 406)

We are aware that some of the infrasubspecific taxa named by Eitschberger already had names, proposed by other authors, and that the formation of their names does not necessarily follow the recommendations of the Code: Appendix D, etc. It is interesting to note, however, that he (cf. pt. 1, p. 170), considered the taxonomic status of *Pieris bryoniae vihorlatensis* Moucha, 1956, doubtful and suggested that it could be identical with *Pieris bryoniae marani* Moucha, 1956, yet further on he named a new infrasubspecific seasonal form of the taxon previously not considered worthy of recognition (pt. 1, p. 173) calling it *postvihorlatensis*. No consequent action was taken following the suspicion of *vihorlatensis* and *marani* being identical.

According to ICZN, all species-group names published after 1930 must in addition to the provisions of Articles 12 and 16 satisfy also those of Article 13(a); these stipulate that an author must provide a statement that purports to give characters differentiating the taxon. Eitschberger's names usually fail to comply with the provisions of Article 13(a), but on a few occasions, a casual reference given to other related taxa might just save some of his names, if the provisions of Article 13(a) are leniently applied. We list below names proposed for species and subspecies, according to rank, in chronological order—monotypic species are denoted here by a binomen even if Eitschberger originally used a trinomen—which, failing to comply with the provision of Article 13(a), must be treated as nomina nuda. The number in parenthesis refers to the page of original designation (in part 1):

Pieris bowdeni (p. 218) nomen nudum
Pieris napi migueli (p. 94) nomen nudum
Pieris napi santateresae (p. 99) nomen nudum
Pieris napi carlosi (p. 103) nomen nudum
Pieris bryoniae schintelmeisteri (p. 129) nomen nudum
Pieris napi muchei (p. 135) nomen nudum
Pieris marginalis tremblay (p. 327) nomen nudum
Pieris marginalis shapiroi (p. 330) nomen nudum
Pieris marginalis browni (p. 332) nomen nudum
Pieris virginensis hyatti (p. 358) nomen nudum
Pieris erutae reissingeri (p. 374) nomen nudum
Pieris erutae kneitzi (p. 380) nomen nudum

We wish to note here, that an earlier named taxon, *Pieris bryoniae tur-*

cica Eitschberger & Hesselbarth, 1977, is nomen nudum owing to the authors' failure to comply with the provision of Article 13(a) of the Code and that this name was not made available in the present work. Also *Pieris angelika* Eitschberger, 1981, was nomen nudum since the name was published without description, definition or valid indication, but this name was made available in the present work.

The following names satisfy the provisions of Article 13(a) usually only because of casual hints included in the description or discussion. These are, therefore, available:

Pieris angelika [nec Eitschberger, 1981] (p. 340): see above.

Pieris steinigeri (p. 382)

Pieris napi kaszabi (p. 137)

Pieris bryoniae wolfsbergeri (p. 154) is available only if a casual reference to the following taxon described subsequently in the same work is accepted as a satisfactory statement purporting to distinguish the taxon (cf. *P. bryoniae lorkovici*, below).

Pieris bryoniae lorkovici (p. 161) is available only if the preceding name is accepted as available. It seems that only some specimens of the two taxa can be separated; some populations are not clearly referable to either taxon (cf. taxonomic comments below).

Pieris bryoniae sheljuzhkoi (p. 128)

Pieris ochsenheimeri gerhardi (p. 228)

Pieris oleracea ekisi (p. 272)

Pieris marginalis reicheli (p. 301)

Pieris marginalis meckyae (p. 322)

Pieris marginalis guppyi (p. 324)

Pieris erutae werneri (p. 380)

Comments on Some Taxa Recognized

This work introduces numerous taxonomic and nomenclatural changes based upon complete intuition. We consider it necessary to discuss the taxonomic status of those taxa, where possible, without another taxonomic revision. For this purpose we retain tentatively a conventional trinominal system of categories (genus, species, subspecies), although we personally are not entirely convinced of the usefulness of the subspecies concept. Thus, the tentative retention of the "subspecies" enables us to better relate some of Eitschberger's taxa. We have excluded all his nomina nuda and with a few exceptions have concentrated on the European taxa. For the same reason, and against our better judgment, we treat here *Pieris napi* and *P. bryoniae* as two polytypic species. We consider that *Artogeia* Verity, 1947, as defined by Kudrna (1974), is a reasonable subgenus of the genus *Pieris* Schrank, 1801, as defined by Klots (1933). Although Kudrna's (1974) elevation of *Artogeia* to generic level was in

accordance with the trend of splitting genera at the time, it must now be seen as an error, as later corrected by the same author (Blab & Kudrna, 1982).

Pieris napi napi maura Verity, 1911 (pt. 1, p. 84) is an unavailable infrasubspecific name proposed for a race, the original combination and rank of which is misinterpreted. The correct name for the taxon should be *Pieris maura* Warren, 1970. Eitschberger's designation of a lectotype is invalid because the lectotype was already designated by Warren (1970) from the original type-series, and can be implied for the species-group taxon. However, Müller & Kautz (1939) elevated Holl's taxon as *Pieris napi blidana* to the rank of subspecies. Should their *blidana* prove to be subjectively identical with *maura, blidana* would have priority.

According to Article 32(c)(i) of the Code, names published hyphenated (except for certain specific cases) must be corrected by the deletion of the hyphen. Eitschberger (p. 87) failed to correct the hyphenated name *Pieris napi-napaeae-atlantis* Oberthür, 1924, to *P. napinapaeaeatlantis* or, which would be more reasonable, to apply to the International Commission on Zoological Nomenclature to use its plenary powers and rule otherwise. Warren (1970) called the taxon *Pieris atlantica* Rothschild, 1917. Specimens called holotype and allotype by Eitschberger are in fact syntypes, as Oberthür made no specific designation.

Both the taxonomic and nomenclatural status of *Pieris napi lusitanica* Sousa, 1929 (or 1926?) (p. 105) is questionable and would be best treated as "nomen dubium". The designation of a neotype of *lusitanica* herein is invalid because (1) the author failed to assure that the type-material of *lusitanica* is lost, and (2) that the specimen which served for the figure [sic] designated the neotype exists and its depository satisfies Article 75 of the ICZN.

Pieris napi napi britannica Verity, 1911 (p. 109) is an unavailable infrasubspecific name. The taxon was treated as a subspecies by Müller & Kautz (1939) who should take the authorship of the subspecies *britannica*. The specimen designated by Eitschberger as a lectotype (pt. 1, p. 109) is referred to as a holotype (pt. 2, p. 402 and pl. 403, figs. 15 and 16) and said to be identical with the specimen figured by Verity (pl. XXXII, fig. 4). A simple comparison of the figures shows that the specimens cannot be identical. Because Verity (1905-11) designated no paratypes, the specimens figured (pt. 2, p. 402, pl. 403, figs. 17-22) and called paratypes cannot possibly have that status.

The authorship of *Pieris napi meridionalis* Heyne, 1895, (p. 114) is long-established (Hemming, 1931); the discussion and erroneous conclusions are totally unnecessary.

The designation of a neotype of *Pieris bryoniae kamtschadalis* Röber, 1907, (p. 126) is invalid because the author failed to ascertain whether the provisions of Article 75 of the Code were fulfilled. It is an open question whether *kamtschadalis* is a subspecies of *bryoniae*. The author's treatment of *kamtschadalis* as a subspecies, originally ranked as a form is correct, but contradicts his treatment of *dubiosa* named by the same author and also designated a form.

The authorship of *Pieris bryoniae* is attributed to Hübner, 1791, (p. 140) who apparently proposed the name uniominally; it is possible that the year 1791 is an error for 1793. According to Kocak (1981) the valid name for the taxon is *Pieris bryoniae* (Hübner, 1806), and *Papilio bryoniae* Hübner, 1793, was placed on the

Index of Rejected Specific Names in Zoology. The notes concerning the supposed type of *bryoniae* must then be seen as irrelevant.

Although we cannot volunteer any statements regarding the taxonomic status of *Pieris bryoniae bryonides* Sheljezhko, 1910, (p. 122, 124) the designation of a neotype is invalid as it was not ascertained if the provisions of Article 75 of the Code were fulfilled.

The designation of a lectotype of *Pieris napi flavescens* Müller, 1933, (p. 151) is invalid because the specimen selected could not form a part of the type-material (syntypes by implication) as it is dated 22 VI 1936.

Pieris bryoniae neobryoniae Müller, 1933 appears to be the valid name for the taxon named *Pieris bryoniae wolfsbergeri* Eitschberger, 1984 (p. 154). The author believed that the name *neobryoniae* was unavailable and overlooked its subsequent elevation to the rank of subspecies. His statements concerning the ICZN made in connection with his naming *wolfsbergeri* are false; he was either unaware of Article 10(b) of the Code or else misinterpreted the facts.

Pieris bryoniae lorkovici Eitschberger, 1984 (p. 161) is surely not worthy of recognition as distinct subspecies (cf. differentiation of *wolfsbergeri* and the preceeding note) and should be treated as a junior subjective synonym of *Pieris bryoniae flavescens* Müller, 1933.

The treatment of *adalwinda* and *bicolorata* (p. 175, 179) as subspecies of *Pieris bryoniae* is not supported by any facts: it is simply stated that this is so and no evidence contradicting the statement is given.

So far as we know, *Pieris napi bryoniae caucasica* Verity, 1908 (p. 184) was elevated to subspecies-rank not later than Müller & Kautz (1939); the authorship of ssp. *caucasica* cannot, therefore, possibly go to "Lorkovic, 1968".

There is no stated logical reason for the treatment of *Pieris balcana* Lorkovic, 1970 [nec 1968, according to Z. Lorkovic's pers. comm.] (p. 202) as subspecies of *Pieris pseudorapae* and we propose to reinstate the taxon to its original rank. We are astonished that the holotype of *balcana* found its way to Eitschberger's private collection (original depository: Coll. Lorkovic, University of Zagreb).

Pieris dubiosa Röber, 1907 (p. 187) is the valid name for the taxon herein called *P. pseudorapae* Verity, 1908. The name *pseudorapae* was proposed by Verity (1905-11) uninominally and ranked "var.". The implied combination is not unequivocal and the name can either be interpreted as subspecific or infrasubspecific; later Verity (1911) treated *pseudorapae* as infrasubspecific race *Pieris napi napi pseudorapae* (Kudrna, 1983). However, the name *dubiosa* has clear priority and its original rank must be interpreted as subspecific according to Article 45 of the Code. Following the valid designation of the neotype of *dubiosa* by Riley and Bowden (1969), it being identical with the lectotype of *pseudorapae* selected by Bowden & Riley (1967), the latter name becomes a junior objective synonym of *dubiosa*.

Pieris napi ochsenheimeri narina Verity, 1908 (or *Pieris napi bryoniae narina* Verity, 1908) is an unavailable infrasubspecific name proposed in quadrinominal combination for a race (p. 221). The name was elevated to the species-rank not later than by Warren (1961) who probably takes authorship.

Pieris melete melete pseudonapi Verity, 1911 (p. 241) is an unavailable infrasubspecific name proposed for race. We are not sure who first raised the taxon to the subspecies-rank, but it was not Verity.

Pieris angelika Eitschberger, 1984 (nec 1981: nomen nudum) (p. 340) was pro-

posed because the author believed that *Pieris napi pseudobryoniae* auct. (nec Verity, 1908) and *Pieris napi arctica* auct. (nec Vertiy, 1908) were both nomina nuda. The reasons for this judgment are an insoluable mystery. Nevertheless, the name *pseudobryoniae* was originally proposed as an unavailable infrasubspecific name for the race *Pieris napi frigida pseudobryoniae* Verity, 1908, and was probably raised to the rank of subspecies not later than by Warren (1961). We know that *Pieris bryoniae pseudobryoniae* (sensu) Warren, 1961, is identical with *angelika* (cf. Eitschberger 1984, pt. 1, p. 21) and has priority over the latter name.

For reasons not stated, *Pieris ergane* Geyer, 1828, a species morphologically closely related to the *P. napi* species-group, is not included in the work under review.

Further corrections of the publication under review would require the undertaking of a proper taxonomic revision of *Pieris napi* species-group, a task far beyond the scope of this paper.

Comments on the Taxonomy of *Pieris napi* Species-group

Pieris napi species-group includes a number of taxa which appear to be actively evolving and shifting adapted modes. Thus distinct biological properties are not always accompanied by the presence of constant and categorical taxonomic characters.

Taxonomic revisions based solely on morphological features are useful in those groups where morphological and biological criteria for the recognition of species are concordant. This is certainly not the case with all "semispecies" of the "superspecies" *Pieris napi* or even the whole *Pieris napi* species-group. Here current active speciation makes the delimitation of sharply defined taxonomic units impossible. This cannot surprise anyone who understands the adaptive processes in animal populations. In such cases morphological features can be utilized primarily for identification using a simple binomen with a clarificatory note concerning the known relationship of the taxon. The approach is more useful than a plethora of speculative trinominal combinations based on intuition and disregard of experimental data. Most reasons making the classification of taxa of the *Pieris napi* species-group difficult were known and explained better 50 years ago (Müller, 1933), than by this work.

The *P. napi* species group has been the object of several biological studies of genetic relationship, including the work of Bowden (1979), Petersen (1949), Lorkovic (1962), and others. In Europe, at least, the group can be described as having complex character shifts of both major and minor gene frequencies for wing pattern and voltinism, all further confused by polyphenism. Additionally, most members are partially interfertile **such that** a mosaic of forms occur. Therefore, it is not surprising that in many cases the identification of any given specimen as belonging to one or another subspecies is speculative and decided either by chance or mysticism. Eitschberger does accept the occurance of inter-

mediate specimens (hybrids), which he prefers to call "heterozygotes", apparently believing the two terms are synonymous, and even goes so far as to describe a certain specimen as "slightly heterozygote" (cf. pt. 1, p. 175).

The view of a lack of understanding of the significance of these intermediates is supported by the fact that although Eitschberger carried out some breeding experiments, and was aware of those carried out by the authors cited above, he leaves these data unutilized and unevaluated.

Although his rejection of transitional units is a rejection of the evolutionary process, the case of the relationship between *Pieris napi* and *P. bryoniae* is one of the best examples of the speciation in progress in Lepidoptera.

Eitschberger seems driven to prove the above two taxa are distinct species, a conclusion based chiefly on the argument that two subspecies cannot coexist in one locality. This would surely be an important observation, if all individuals could be clearly distinguished by biological markers as belonging to one or the other species. His categoric rejection of the possible contemporary conspecifity of *napi* and *bryoniae* is not only the rejection that at least some gene flow is in fact possible, it is the rejection of an important adaptive process.

A clear taxonomic synopsis of the *Pieris napi* species-group would have surely enabled biologists without special taxonomic knowledge to carry out field studies that could have contributed to the advancement of our knowledge not only of the pierids concerned, but of their biological and ecological relationships. This unrefereed work produces quite the contrary. It provides the completely unsubstantiated illusion that the vast coterie of named entities have some biological substance. Even more unfortunate is a sort of implied validation of bad science by the sheer volume of information which could mislead the uninitiated.

Conclusions

On its merit, this work is suitable for inclusion in the Official Index of Rejected Works, and we deeply regret that it was ever published, because it brings the sciences of taxonomy and lepidopterology into disrepute.

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Editor's Note: It has been called to our attention that this work served as a thesis accepted in fulfillment of the Dr. Phil. degree in Zoology at the University of Bonn, West Germany.

Discovery of Two New Species and Genera of Shaggy Tortricids Related to Synnoma and Niasoma (Tortricidiae: Sparganothini)

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The monotypic genera *Synnoma* (Walsingham, 1879) and *Niasoma* (Busck, 1940) are represented by two of the most unusual species in North American Tortricinae. *Synnoma* displays structural characters, particularly in male genitalia, that appear to associate it unequivocally with Sparganothini; but *Niasoma* has remained enigmatic and has been accorded independent tribal status, primarily for lack of convincing evidence as to its relationships (Powell, 1983). Hence, the discoveries in recent years of the larva of *Niasoma*, together with two previously undescribed species that show similarities to the two described, aberrant genera, have considerable relevance to our understanding of systematic relationships in this group.

Synnoma lynosyrana, which was originally described from northern California and occurs widely in arid regions of the western U.S., is a highly modified species. The diurnal moths emerge in late fall and are sexually dimorphic; the females are flightless. The adults possess a rudimentary tongue and apparently do not feed; females deposit imbricate masses of eggs typical of the tribe Sparganothini but cover them with a black colleterial substance unlike any other known in the subfamily. The larvae feed colonially from tough silken webs on *Gutierrezia* and *Chrysothamnuus* (Asteraceae) (Powell, 1976).

Niasoma metallicana (Walsingham, 1895) was described from Florida and occurs in the Gulf States, but it has remained poorly known. The species was first reared in 1982, affording the opportunity to compare relationships based on larval characters. Adults of *Niasoma* possess thick vestiture on the body and rows of upraised scales on the forewings, rendering a shaggy appearance similar to that of *Synnoma* (Powell, 1976, figs.), much of which is lost from flown individuals. *N. metallicana* is particularly remarkable in this respect; reared specimens have erect bunches of scales up to 1.5 mm in length protruding at right angles to the plane of the forewing. Previously examined specimens in collections have only traces of the erect scaling, having lost most of it either in flight or handling. Adults of the two new species described below show similar traces of

upraised scaling and presumably have a ruffled appearance when freshly emerged.

Neither *Niasoma* nor the new genera display sexual dimorphism as strongly as does *Synnoma*, but *N. metallicana* and *Synalocha gutier-reziae*, n. sp., have two color phases in both sexes. Both these species are multivoltine, a further parallel as contrasted with *Synnoma*.

Synalocha Powell, new genus

Type species.—Synalocha gutierreziae Powell, **new species.**

Adult.—**Head**: Antenna in male thickened, serrate, with elongate setulae (fig. 2); simple with minute setulae in female; dorsal scaling in a single band per segment. Labial palpus elongate, II segment only slightly curved, enlarged 2 X at basal ⅓; III segment straight, ½ as long as II (fig. 3). Maxillary palpus rudimentary, no differentiated segments. Ocelli and chaetosema well developed. **Thorax**: Tarsal segments without enlarged bristles. Forewing moderately narrow, slightly broader in the larger female. No costal fold in male. Chorda absent; stem of M in cell weak, with remaining trace ending at M_2; Cu_2 present; R_4 and R_5 stalked, R_4 to costa, R_5 to termen; M_3 and Cu_{1a} separate. Upraised rows of scales in transverse pattern. Hindwing with 9 veins to margin; humeral vein absent; Sc + R and Rs stalked; R_5 and M_1 closely approximate; M_3 and Cu_1 closely adjacent; 1A a trace. No costal hair tuft in male. Cu with hair pecten. **Abdomen**: Dorsal pits absent. Male without coremata. Female with moderately enlarged corethrogyne scaling. Male genitalia (fig. 6): Uncus short, tapered, curved, strongly sclerotized. Saccus undifferentiated, lateral arms of vinculum joined by membrane. Socii buttonlike, flat, oval, setate, unscaled. Gnathos arms separate, spinulose. Transtilla moderately broad, serrate, separate from pulvinus. Valva simple, pulvinus weak; sacculus and costal rim sclerotized, narrow rims. Aedeagus strongly curved from short phallobase, flared distally, with a blunt external spur; vesica with 6 elongate cornuti (presumed deciduous). Female genitalia (fig. 9): Papillae anales narrow, slightly enlarged anteriorly and posteriorly, without specialized setae. Sterigma a wide, simple bowl, with deep, enlarged antrum subtending. Ductus bursae without colliculum or accessory sac, thickened basally and longitudinally with parallel ribs; corpus bursae well differentiated, without accessory pouch or scobination; signum thornshaped without capitulum.

Final instar larva.—Sharing Sparganothini characters as defined by MacKay (1962:29). **Head**: Ocelli (stemmata) I, II, and VI subequal to or slightly larger than III-V. Adfrontals narrow basally, broader posteriorly, the sutures sinuate. **Thorax**: D and SD pinacula on meso- and metathorax not or only slightly elongated posteriorly. SV group on meso- and metathorax with a single seta. **Abdomen**: SV group on A1, 2, 7, 8, 9 with 3, 3, 3, 2, 2 setae; SD_1 on A8 directly anterior to spiracle; D_1's of anal shield anterior to and about as far apart as each is from its corresponding SD_1; L_3 on A9 occasionally lacking. Anal shield distinctly triangulate posteriorly, strongly sclerotized laterally; anal fork well developed. Spiracles small, those of A3-7 ca 0.04-0.05 mm in diameter, A8 ca 0.12 mm. Crotchets variably biordinal, 42-48 on abdominal, 38-40 on anal proleg.

This genus is most similar and presumably closely related to *Synnoma*

Walsingham, although differing in several aspects of the genitalia. *Synalocha* is aberrant compared to other Sparganothini, with reduced socii, separated vinculum anteriorly and flared aedeagus. In the female, the enlarged, sclerotized antrum, reminiscent of *Acleris* (Tortricini), is unique among Sparganothini.

Synalocha gutierreziae Powell, new species

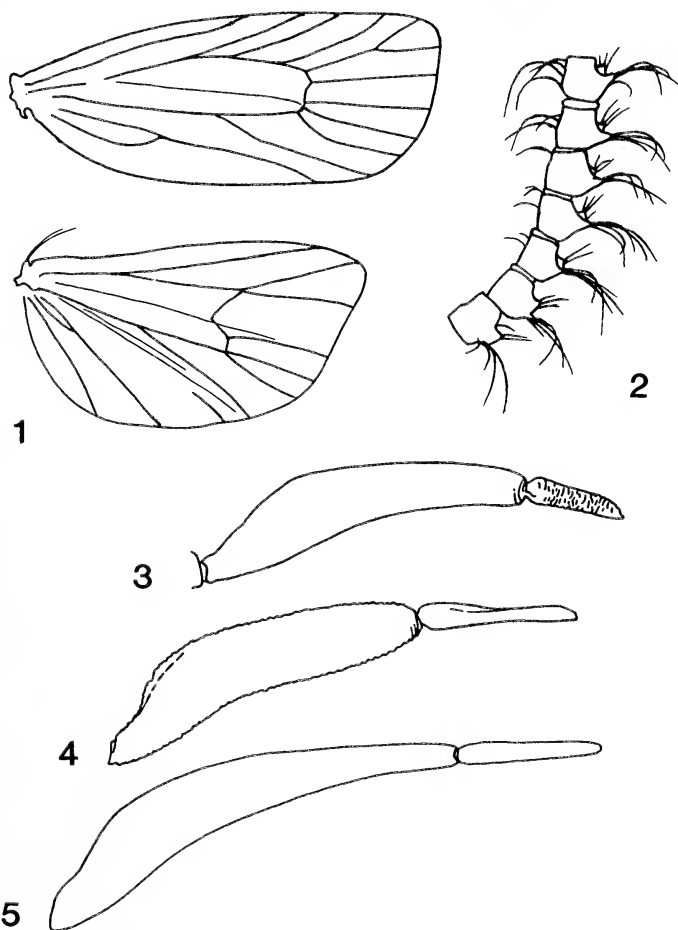**Male.**—Length of forewing 6.5-7.9 mm (lab reared). **Head:** Antenna enlarged,

Fig. 1.   Wing venation of *Syllonoma longipalpana* Powell.
Fig. 2.   Antennal segments of *Synalocha gutierreziae* Powell.
Figs. 3-5.   Labial palpi, segments II-III: 3, *Synnoma lynosyrana* (Wlsm.); 4, *Synalocha gutierreziae*; 5, *Syllonoma longipalpana*.

strongly serrate with elongate whorls of setulae (1.6 × segment width) on ventral half (fig. 2), width of basal segments ca 0.23 eye diameter. Labial palpus elongate, II segment broadened at basal ⅓, length 2.10-2.25 × eye diameter; III 0.47-0.55 as long as II; scaling moderately spreading, dark gray-brown with a few pale red-brown scales intermixed. Tongue short, probably functionless. Crown with very short postantennal spurs; scaling dark brown intermixed with pale brown, especially towards occipital tufts, overhanging to labial palpi, obscuring front. **Thorax**: Dorsal scaling entirely pale tan to mostly dark brown with pale tan tegulae. Underside and legs pale tan tinged with brownish to dark brown tinged with blackish, tarsal segments with pale apical bands. **Forewing**: Moderately narrow, length 2.7 to 2.8 times width; costa nearly straight, slightly bowed near base, apex blunt, termen nearly straight, dorsal margin strongly curved near base. Scaling shining, pale tan, with a faint to moderately well defined pattern of pale reddish brown, emphasized by scattered, slightly upraised darker scales, blackish in darker specimens: costa at base, a suggestion of a basal band usually indicated by slightly raised tufts in cell; a transverse band from mid-costa outwardly oblique through outer part of cell to dorsal margin before tornus; an outer costal spot before apex extending to R_{4+5} stem; an ill-defined marginal line at base of fringe, which is pale tan even on dark specimens. Underside dark brown with pale tan margins crossed by dark strigulae in darker specimens. **Hindwing**: Apex rather acute, termen shallowly emarginate. Dorsal scaling dark gray-brown, only slightly paler in specimens having pale thoracic and forewing scaling. Fringe pale tan. Underside similar, paler. **Abdomen**: Tan to dark brownish gray, each segment with posterior pale scale bands; underside similar. Genitalia as in fig. 6 (drawn from paratype, Jal, NM, JAP prep. no. 4978, 4n).

Female.—Length of forewing 6.5 to 10.5 mm. Generally as described for male; forewing slightly broader, length 2.6-2.7 times width. Similar to male in color variation, usually paler, dark form with blackish body and hindwing scaling rare in females (5 of 19 specimens), hindwing usually pale gray-brown. Abdomen with enlarged dorsal and lateral scale tufts forming a hood over papillae anales, dark brown tinged with purplish. Genitalia as in fig. 9 (drawn from paratype, 10 mi E Ft. Stockton, TX, JAP prep. no. 4457, 4n).

Holotype male.—TEXAS: 5 miles north of Monahans, Ward Co. 4 July 1979, reared from silk webbing on *Xanthocephalum sarothrae* (J. K. Wangberg coll. 057-01); allotype female, Texas: 2.5 miles E of Wink, Winkler Co., V-1980 "on perennial broomweed *Gutierrezia* spp." (B. R. McPherson coll. 043-04) deposited in Essig Museum of Entomology, U. California, Berkeley. Paratypes (23 males, 17 females): ARIZONA, 40 mi NE Clifton, Greenlee Co. ca 4500′, 2 males, 1 female X-9-65, larvae webbing flowerheads of *Gutierrezia sarothrae* (B. Freeman). NEW MEXICO, Jal, Lea Co., 2 males, 2 females X-15-79 (B. R. McPherson). Roswell, Chaves Co., 1 female "Aug. 22" (T. D. A. Cockerell). TEXAS, same data as allotype, 3 males, 4 females (McPherson colls. 030-04, 043-04, 044-04); 10 mi W Wink, Winkler Co., 1 female VII-4-79, r.f. silk webbing on *Xanthocephalum sarothrae* (J. K. Wangberg coll. 059-01); same data as holotype, 1 male; 10 mi S Monahans, Ward Co., 1 male VII-5-79, r.f. silk webbing on *X. sarothrae* (Wangberg coll. 064-01); 10 mi E Ft. Stockton, Pecos Co., 1 male, 5 females IX-15-78, *X. sarothrae* (Wangberg coll. 046-01). "Brenster Co" [Brewster Co.], 7000 ft., 13 males, 3 females "5/26" (ex Meyrick Coll.). Paratypes deposited in collections of BM (NH); Texas Tech University, Lubbock; Essig Museum, U. California, Berkeley; and USNM. Additional specimens from Ft. Stockton in poor condition

were examined but not designated as paratypes.

Most of the New Mexico and Texas localities are situated along an 85-km north-south transect of the Pecos River Valley, a reflection of sampling effort by Dr. Wangberg and his associates. The record from extreme eastern Arizona indicates that *S. gutierreziae* is much more widespread. It is curious that there were no specimens in American collections prior to 1965. Those in the Meyrick collection had been misidentified as *Synnoma lynosyrana*; hence this distinctive species was overlooked.

Biology.—All the recently collected specimens have been reared from larvae collected on *Gutierrezia sarothrae* or *G. microcephalum* (Asteraceae, Asteridae). Although some are labelled *Xanthocephalum* sp. or *X. sarothrae*, *Gutierrezia* is the valid generic assignment according to present concepts (Lane, 1984). *Synalocha gutierreziae* has been the subject of biological studies by J. K. Wangberg and D. R. Edwards of Texas Tech University for several years. They provided the following synopsis of the detailed study, which will be reported separately.

The species is multivoltine, in contrast to the univoltine *Synnoma lynosyrana*, adults of which emerge in October and November (Powell, 1976; Wangberg & Edwards in litt.). Males fly readily, while females appear to be too heavy to fly, as is true of *S. lynosyrana*. Dissections of unmated *S. gutierreziae* females revealed whitish material in the colleterial glands, in contrast to the black substance produced by *S. lynosyrana*. Wangberg and Edwards found that the eggs are green, deposited in rows along the upper surface of leaves; in the lab they are laid in patches, with scale tufts deposited at one end. There are 7 larval instars, and pupation occurs inside tied leaves, in a shelter that is not as strong as the tough webs of *S. lynosyrana*.

Syllonoma Powell, new genus

Type species.—**Syllonoma longipalpana** Powell, new species.

Head: Antenna serrate in male with long setulae (ca 1.0 segment width) in dense whorls from ventral half of enlarged segments; dorsal scaling in a single band from base; simple with minute setulae in female. Labial palpus slender, greatly elongate, II segment ca 4 × eye diameter, III ca 0.3 as long as II (fig. 4). Maxillary palpus apparently rudimentary. Ocelli and chaetosema well developed. **Thorax**: Tarsal segments without enlarged bristles. Forewing moderately broad. No costal fold in male. Wing venation as in fig. 1: Chorda absent; stem of M present in cell without trace of fork, ending at M_2; Cu_2 present; R_4 and R_5 stalked, R_4 to costa, R_5 to termen; M_3 and Cu_{1a} separate. Upraised scales in transverse rows. Hindwing with 9 veins to margin; humeral vein absent; Sc + R and Rs stalked, without crossvein; R_5 and M_1 connate; M_3 and Cu_1 connate; 1st A present. No costal penicillus in male. Cubital hair pecten present, weak. **Abdomen**: Dorsal pits absent. Male without coremata; female apparently without corethrogyne scale tufts. Male genitalia (fig. 7): Uncus curved, strongly sclerotized, deeply cleft apically, without ventral hair tuft; saccus not differentiated; no subscaphium and hami; apparently socii reduced to a few setae, gnathos arms separate, weakly sclerotized, setate; transtilla broad, with an elongate projection anteriorly, non-dentate; valva simple, sacculus a sclerotized ridge, attached across valva distally to the weakly sclerotized costal rim; pulvinus weak, no clasper; aedeagus elongate, evenly curved, strongly flared distally, vesica with 2 slender, deciduous cornuti, apparently
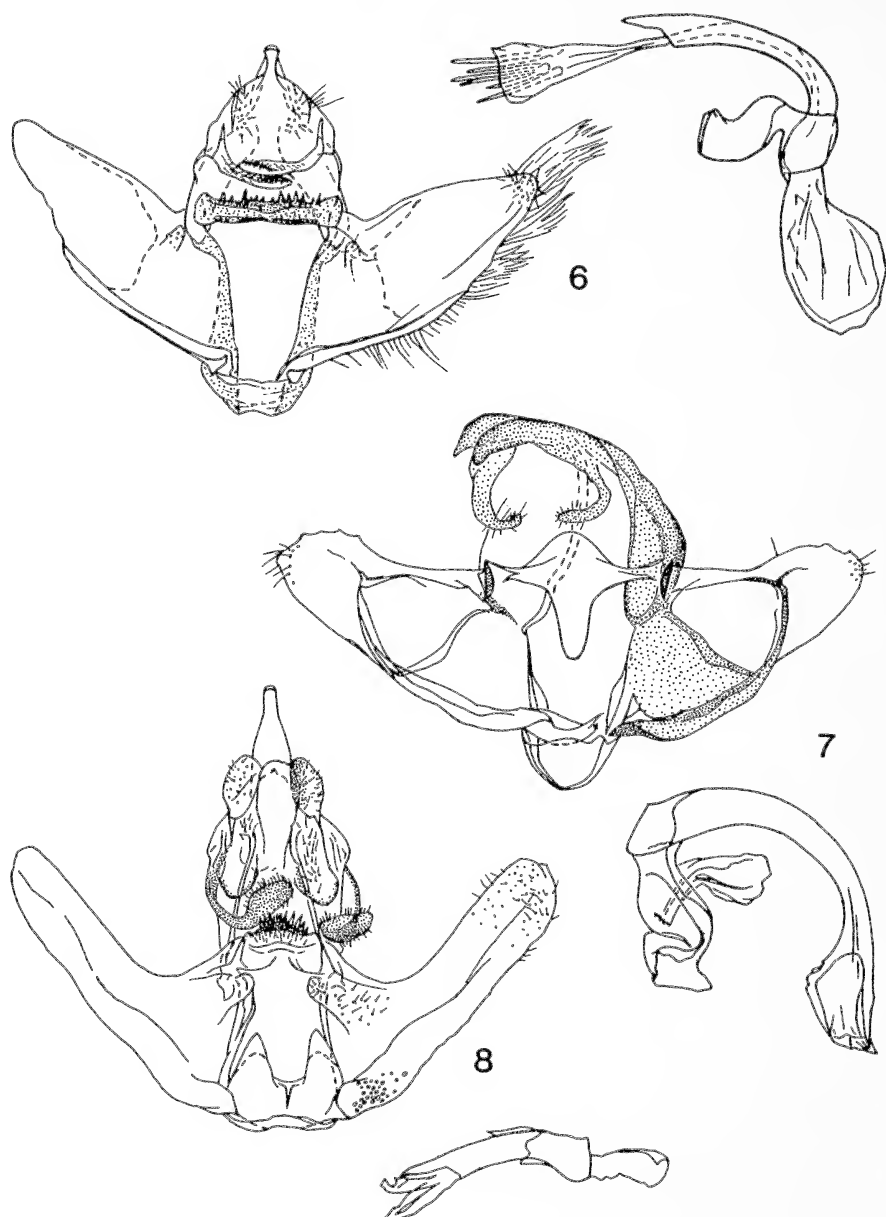
Figs. 6-8.   Male genitalia, ventral aspect, valvae spread, aedeagus removed and shown in lateral aspect: 6, *Synalocha gutierreziae* Powell; 7, *Syllonoma longipalpana* Powell; 8, *Synnoma lynosyrana* (Wlsm.).

attached basally. Female genitalia (fig. 10): papillae anales narrow, slightly enlarged anteriorly, without floricomous setae; sterigma a shallow V-shaped ridge, sclerotized interiorly to antrum, subtended by a second, external V-shaped ridge; antrum enlarged but not sclerotized; ductus bursae membranous, gradually widened distally, without accessory sac; corpus bursae well differentiated, without accessory pouch, signum a single invaginated, slender horn.

Larva unknown.

The new genus is most similar and apparently closely related to *Synalocha,* which *S. longipalpana* resembles superficially, in wing venation and male genitalia, especially the form of the uncus, reduced socii, gnathos and aedeagus. *Syllonoma* differs markedly, however, in the transtilla form (which is almost exactly like that of the cnephasiine, *Decodes lundgreni* Powell) and the valva and sacculus, which are unlike those of any other Sparganothini. Female structures of the two genera are generally similar, although the sterigma and antrum form differ, and evidently *S. longipalpana* lacks corethrogyne scaling and correlated oviposition behavior.

Syllonoma longipalpana Powell, new species

A small, dark species with tan forewings with transverse dark brown bands in the male and weakly upraised scale ridges in both sexes. The long, slender palpi are unique among American Tortricinae.

Male.—Length of forewing 6.4 mm. **Head**: Labial palpus elongate, slender, II segment enlarged to 2 × basal diameter near base, only slightly curved. Scaling appressed, brownish black with a few, scattered red-brown scales. Scaling of crown roughened, dark brown with scattered red-brown, concentrated medially. **Thorax**: Dorsal scaling concolorous with head. Underside and legs shining blackish brown. **Forewing**: Length 2.3 times width, rectangulate, costa nearly straight, termen gently curved, dorsal margin strongly curved near base. Ground color dark tan with scattered brown scales and 3 broad, dark brown, transverse bands (probably upraised in fresh specimens), first at base, second from costa outwardly angled to dorsal margin before tornus, and the third subapically towards termen above tornus; the latter two indistinct and coalesced toward tornal area; a thin brown line in apical area. Fringes lacking from holotype. Underside dark brown with tan areas of upperside indicated in costal area. Hindwing entirely dark brown, reflecting bluish. **Abdomen**: Color not recorded. Genitalia as in fig. 7 (drawn from holotype, JAP prep. no. 5051, one preparation examined).

Female.—Length of forewing 7.3 to 7.6 mm. Essentially as described for male except generally darker brown. Forewing brown, weakly showing transverse bands of male, with numerous parallel rows of upraised scales in both darker and paler transverse band areas. Genitalia as in fig. 10 (drawn from allotype, JAP prep. no. 5066, 2 preparations examined).

Holotype male and allotype female, SOUTH CAROLINA, Myrtle Beach, Horry Co., July 9, 1943 and August 14, 1943 (C. T. Parsons) deposited in MCZ. One female paratype, NORTH CAROLINA, Leland, Brunswick Co., June 17, 1946 (O. Buchholz) in ANSP.

Superficially this species resembles females of *Platynota idaeusalis*

(Walker), but apparently it has less pronounced sexual dimorphism, lacks the male costal fold, and has conspicuously longer labial palpi. The two localities, which are about 96 km apart, are coastal sites, and populations might be expected all along the southeast Atlantic Coast.

It is strange that more specimens have not been discovered. None was represented in material accumulated by R. L. Lambert during his revisionary work on the Sparganothini, nor were there any in the extensive Florida collections of C. P. Kimball examined at MCZ in 1982, where the types were discovered in other unsorted material.

Systematic Relationships

Synnoma lynosyrana is markedly divergent from most Sparganothini in several biological and correlated morphological features (Powell, 1976). The genitalia, however, are characteristic of typical members of the tribe. The male of *S. lynosyrana* is similar to *Platynota*, differing by having sclerotized gnathos arms which are enlarged, paddle-like distally (fig. 8, drawn from JAP prep. no. 3085, Frazier Park, CA, 10 preparations examined). The female genitalia, excepting the enormous colleterial glands, are like many *Sparganothis* and *Platynota* (fig. 11, drawn RL prep. 545, Douglas, AZ, 15 preparations examined). Each of the new genera displays aspects of divergence from the usual sparganothine pattern, and in some respects they bridge the gap formerly separating *Niasoma* from other members of the tribe.

Synalocha (fig. 6) shows sparganothine affinities primarily in the free gnathos arms, but differs by having reduced socii, the vinculum joined only by a membranous band anteriorly, and by the flared aedeagus distally. *Syllonoma* (fig. 7) is still more aberrant for the tribe, having a deeply cleft uncus, extremely reduced socii, and a large flap-like transtilla. Its loss of socii and flared aedeagus appear to show relationships to *Synalocha* and to *Niasoma* (figured by Busck, 1940; 3 JAP preps. examined). The uncus, transtilla and sacculus ridge crossing the valva in *Syllonoma* are unlike any known corresponding characters in other sparganothine genera. Females of the four genera are more conservative, as is true throughout the tribe, and each shows marked modifications of the sterigma and associated structures, with a relatively undifferentiated ductus bursae (figs. 9-11; Busck, 1940).

The wing venation is quite similar in all four genera (fig. 1).

Larvae identified as those of *Synalocha gutierreziae* were collected and sent to me by D. R. Edwards, although associated, reared adults from the same locality were not provided (5 mi S. Kermit, Winkler Co., TX, 9-8-82, DRE 108-07, on *Gutierrezia*). Larvae of *Niasoma metallicana* were obtained from D. H. Habeck, along with reared adults (Edgecliffe, Alachua Co., FL, VIII-17-82, reared from *Eupatorium capillifolium*, R. Weston & J. Gillmore, DHH rearing A3116d). These were compared to larval characters of *Synnoma lynosyrana*, using the description by MacKay
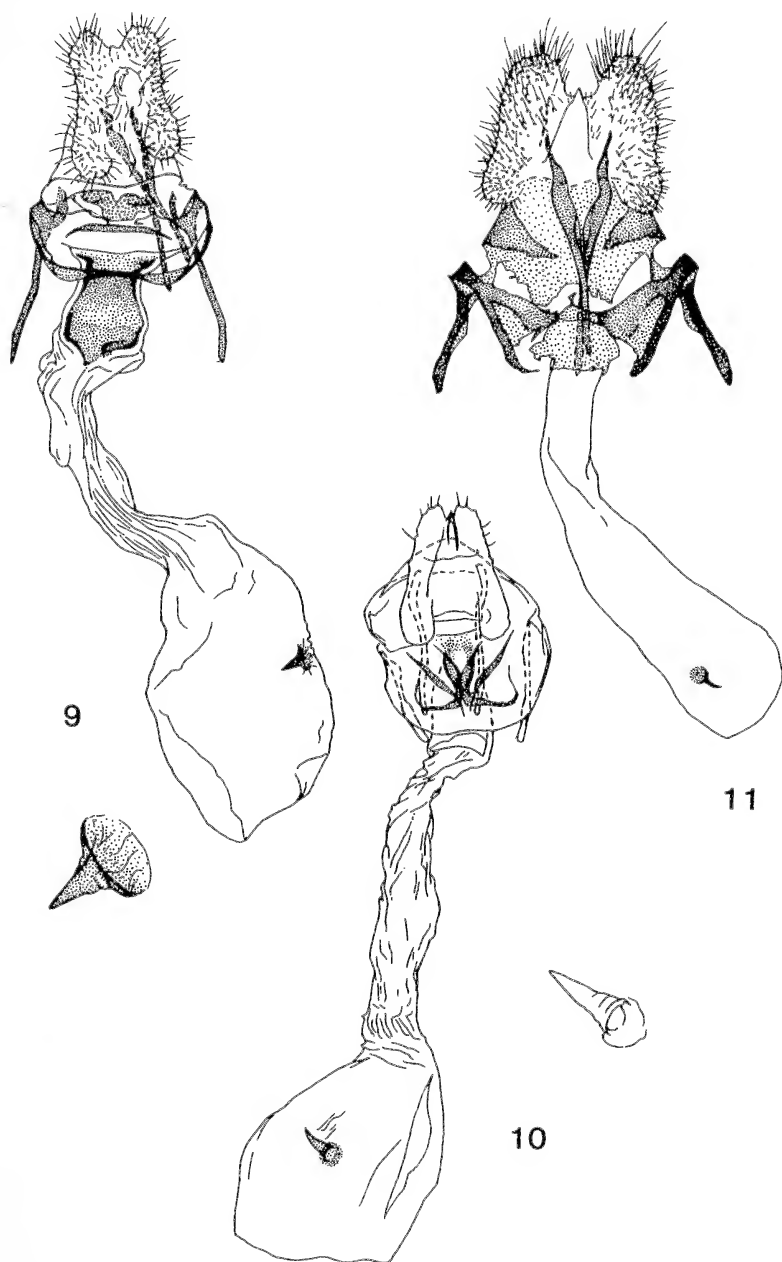
Figs. 9-11. Female genitalia, vental aspect: 9, *Synalocha gutierreziae* Powell; 10, *Syllonoma longipalpana* Powell; 11, *Synnoma lynosyrana* (Wlsm.).

(1962) (Calif. and Montana specimens) and larval specimens from northern California and Nevada (JAP 58H3, 73H8, see Powell, 1976 for data).

All three genera match the diagnostic characters of Sparganothini defined by MacKay (1962): On the head, seta P_1 is closer to P_2 than to Adf_2, with P_1 at the apex of an obtuse angle formed with the other two setae; the V_1 setae on abdominal segment 9 are distinctly farther apart than those on A8 and usually A7. *Niasoma* has P_1 closer to P_2 than in the other genera, a stronger sparganothine tendency but has V_1's of A9 and A7 equidistant, a weaker indication of affinity with the tribe (i.e. more Archipini-like).

Niasoma also has ocelli I, II, and VI smaller than III and IV, has slightly larger spiracles than does *Synnoma*, and has D and SD pinacula of the mesothorax elongated posteriorly. These are features more characteristic of typical sparganothines and some Archipini than of *Synnoma*. Both *Niasoma* and *Synalocha* differ from *Synnoma* in having the anal shield distinctly triangulate posteriorly and seta SD_1 on A8 directly anterior to the spiracle.

On the basis of the resemblance of *N. metallicana* to *Synalocha gutierreziae* and *Syllonoma longipalpana* in several genital features and particularly the adherence of the larvae to diagnostic features of Sparganothini, I regard *Niasoma* and the two new genera as aberrant members of this tribe. Both Walsingham (1895) on the basis of external characters and wing venation, and Busck (1940), on genitalia, treated *Niasoma* as sparganothine. Lambert (1950), however, excluded it from the tribe, and Obraztsov (in MS) regarded *Niasoma* as representing a monobasic tribe.

The three species of this group for which larval foodplants are known feed on Asteraceae (Compositae). The four genera of moths appear to be derived forms relative to typical Sparganothini and generalized Archipini. Thus, radiation of Asteraceae, a family generally regarded as derived by plant evolutionists, appears to have set the stage for speciation in this line of Tortricinae. This is in accordance with my hypothesis that major lines of Lepidoptera evolved with ecological horizons rather than major angiosperm taxa, and only lesser, derived taxa have developed in association with particular orders of plants (Powell, 1980).

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Notes

Oviposition records and larval foodplants of butterflies in the Atlas Mountains of Morocco

Larval foodplants have been recorded for some Moroccan butterflies, but knowledge of them is still poor (Higgins & Riley, 1980; Rungs, 1981). A substantial proportion of species have no recorded hostplants, and many that do probably also feed on other unrecorded plant species. We visited the Middle and High Atlas in Morocco during May and June 1982 to record oviposition and larval hostplants, mostly of Lycaenids. The results are presented in Table 1.

Most of these butterflies occurred only where their hosts grew in particular situations. For example, *Cigaritis allardi* tended to lay upon smaller than average (<40 cm diameter and <35 cm tall), somewhat isolated *Cistus salvifolius* plants, despite being adjacent to extensive, dense, tall stands of *C. salvifolius*. *Plebejus martini* laid mostly on *Astragalus incanus* plants growing adjacent to bare ground. *Scolitantides bavius* Eversmann eggs were found only on 1-2 cm tall buds of large (>300 cm^2) *Salvia argentea* specimens.

Euphydryas desfontainii Godart laid batches of one to three eggs on the undersides of *Knautia* leaves. *E. aurinia* Rott. in Britain lays much larger egg clusters (often 200 or more; Porter, 1981). In North America, *Euphydryas* also varies in this respect within and between species (Ehrlich et al., 1975; M. C. Singer, pers. comm.).

It is interesting that certain not-closely related plant families (in different orders; Heywood, 1978) are used as larval foodplants by several Lycaenids, but that those used do come from a restricted suite of plant families; mostly Leguminosae, Cistaceae, Geraniaceae, Ericaceae and Labiatae in Morocco. For example, Leguminosae and Cistaceae are probably used by *Cigaritis allardi* and *Lampides boeticus*, Leguminosae and Labiatae by *Pseudophilotes abencerragus*, Cistaceae and Geraniaceae by *Aricia agestis*, and Leguminosae and possibly Ericaceae by *Plebejus martini* (*P. martini* also occurs in heathy places; Higgins & Riley, 1980). British *Plebejus argus* use Leguminosae, Ericaceae, Cistaceae and occasionally Labiatae (Thomas, 1983), whilst the endemic Moroccan *Plebejus vogelii* feeds upon *Erodium cheilanthifolium* (Geraniaceae) (Rungs, 1981).

It is unclear whether these plant families share particular mechanical or biochemical attributes (e.g. high Nitrogen and water, or low tannins). Many Lycaenid larvae specialise on soft nutritious meristematic and reproductive growth (Robbins & Aiello, 1982; Thomas, 1983; Chew & Robbins, 1984). Considering the breadth of diet of some species, it seems likely that the nutritional or mechanical attributes of the foodplants may be more important than secondary compounds in determining which species are included in their diets. Alternatively, they may just happen to be the most abundant dicotyledonous plant families in habitats favoured by these Lycaenids for other reasons.

Because these plant families are often unrelated, a coevolutionary explanation (Ehrlich & Raven, 1964) does not provide a convincing explanation for host use by many Lycaenids.

Research Ltd., Atlas Hirepurchase, and Worldwide Butterflies Ltd. Rudi Mattoni kindly gave us access to unpublished oviposition records. We are also very grateful to A. O. Chater (BMNH) for determining plant specimens.

Note. Butterfly nomenclature follows Higgins & Riley (1980), except where butterfly authors are given.

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Table 1. Larval foodplants and oviposition records for butterflies in the Atlas Mountains of Morocco. Records given in brackets are those quoted by Rungs (1981) and Higgins & Riley (1980). Unpublished records of R. Mattoni (*in litt.*) are marked with *. E = eggs found in wild, no oviposition seen. 0 = oviposition in wild. P = oviposition in wild and subsequently plant was acceptable to first instar larvae in captivity. L = wild larvae found feeding.

Butterfly		Foodplant	Locality	Altitude
PAPILIONIDAE				
Zerynthia rumina	P	*Aristolochia longa* L. subsp. *paucinervis* (Pamel) Batt.	1	1400 m
	E/P/L	*Aristolochia* species (*A. boetica*)	2, 8	1600-2100 m
PIERIDAE				
Aporia crataegi	L	*Crataegus laciniata* Ucria (*C. monogyna, Pierus malus* & *P. communis*)	3	2100 m
Colias crocea	O	*Medicago polymorpha* L.	1	1100 m

	O	*M. sulcata* Desf. (*M. sativa, M. lappacea & M. hispida*)	1	1100 m
LYCAENIDAE				
Cigaritis zohra	P	*Coronilla minima* L.	2	1600 m
C. allardi	O	*Genista quadriflora* Munby	4	1500 m
	O	*Cistus saqlvifolius* L.	4	1500 m
Lycaena phlaeas	O	*Rumex thyrsoideus* Desf. (*Rumex*)	2	1600 m
Tomares ballus	O	*Medicago* cf. *turbinata* (L.) All. (*Anthyllis tetraphylla, Erophaca boetica*)	1	1100 m
Lampides boeticus	P	*Onobrychis peduncularis* (Cav.) DC.	2	1600 m
	E/L	*Lotus moroccanus* Ball	1	1600 m
	P	*Trifolium angustifolium* L.	4	1500 m
	O	*Cytisus megalanthus* Pam. & FontQuer.	9	2350 m
	O	*Helianthemum helianthemoides* (Desf.) Grosser (*Dolychos lablab, Phaseolus vulgaris, P. multifolorus, Cajanus indicus, Spartium junceum & Cytisus battandieri*)	2	1600 m
Cupido lorquinii	E/P/L	*Anthyllis vulneraria* L.	1, 2, 4, 9, 10	1400-2600 m
	O	*Anthyllis* species*	2, 11	
Glaucopsyche melanops	E/P/L	*Ononis atlantica* Ball	1	1500 m
	O	*Adenocarpus anagyrifolius* Cossan & Bal	8	1700
Pseudophilotes abencerragus	P	*Medicago* cf. *turbinata* (L.) All.	1	1100 m
	O	*Thymus* cf. *hirtus* Willd.	1	1600 m
	O	*Salvia taraxicifolia* Cossan ex Hook. f.	8	1700 m
	O	*Thymus* species*	2	
Scolitantides bavius Eversmann	E/O	*Salvia* cf. *argentea*	2	1600 m
	E	*Salvia argentea** (*Salvia argentea*)	2, 11	1600-1900 m
Plebejus martini	E/P/L	*Astragalus incanus* subsp. *incurvus* (Desf.) Chater	1	1500
	O	*A. incanus**	12	
Aricia agestis cramera	O	*Erodium* species	6	2100 m
	O	*Erodium* species (Geraniaceae, *Helianthemum*)	8	1900 m
Polyommatus (Agrodiaetus) thersites Cantener	P	*Onobrychis peduncularis* (Cav.) DC.	2	1600 m
	O	*Onobrychis* species* (*Onobrychis*)	2	
P. (Lysandra) punctifera Oberthur	E/O/P/L	*Hippocrepis scabra* DC.	2	1600 m
	O	*H. scabra** *P. (plebicula) atlanta*	2, 12	1600-2150 m 2100 m
	O	by 1 female on *Onobrychis* species*	6	

courting model males for mimicking conspecific males. This potential confusion would be compounded because of frequency-dependence (i.e. model males would be more common than mimic males) and because Batesian mimicry can involve behavioral subtleties such as flight patterns or the choice of a microhabitat. At best, a female's confusion. . .would lead to a waste of her time and energy. . ." Observations of such interactions are, however, remarkably rare in the literature.

Diurnal flight has evolved twice in the *Drasteria* group of Noctuid moths. In each case there is a strong resemblance to sympatric and synchronic butterfly species which fits the general picture of Batesian mimicry: the butterflies (models) are phenotypically normal while the moths (mimics) depart markedly from the appearance of their relatives, in phenotype as well as in behavior. The "Blue Moth," *Caenurgina caerulea* Grt., is common in spring in foothill and lower montane habitats in California, flying sympatrically and synchronically with the Lycaenid *Celastrina argiolus echo* Edw. and other less common Blues. Two very similar species of *Euclidea—E. cuspidea* Hbn. in the East and *E. ardita* Franc. in the Western part of the United States and southern Canada—co-occur in spring with skippers of the genus *Erynnis* (Hesperiidae), from which they may be distinguished in flight only with difficulty. I have seen male *C. a. echo* investigate *C. caerulea* in the air, but never a courtship *per se* involving these species.

A male *Erynnis propertius* Scud. & Burg. was watched for over 3 min, beginning at 1305 hrs, 17 April 1984, as it courted a female *Euclidea ardita* in the understory of riparian oak woodland at Rossmoor Bar, Rancho Cordova, Sacramento County, California. The moth's flight was characteristically slow; it lit about four times but was immediately nudged into flight by the male's attempts at copulation. In the air the male hovered behind the female in the normal manner for *Erynnis* courtship, and it was not realized that the interaction was interspecific until the moth first lit. She took no apparent evasive action, but the pair was ultimately lost as they flew into thick shrubs. *Erynnis tristis* Bdv. was common in the area (about 20 seen); the *E. propertius* was the only example of its species seen. About ten *Euclidea* were seen flying in dappled light and shade in the area. Weather conditions were: scattered cumulus, air temperature ca. 22°C, SW wind 15 km/h. Insofar as I can determine, *Euclidea* courtship is undescribed. To a human observer, a male *Erynnis* is rather easily recognized by its rapid flight and territorial behavior, but females are virtually indistinguishable from *Euclidea* in the air—the resting posture, however, is easily diagnostic.

The basis for the inference of mimicry in *Caenurgina* and *Euclidea* is purely contextual, as neither of the presumed models is known or even suspected to be distasteful. However, there is increasing recognition that mimicry may be based on forms of undesirability other than unpalatability. The differential flight characteristics of *Erynnis* and *Euclidea*, for example, suggest that a poor probability of capture and a poor ratio of energy expended in pursuit to energy reward from capture would make *Erynnis* an undesirable or at least low-priority prey item. A case of this sort was described by Hespenheide (1973, J. Entomol. (A) 48:40-56) involving mimicry of elusive, swift-flying Dipterans by beetles.

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Notes on *Erebia occulta* (Lepidoptera: Satyridae)

Readers of this journal who do not follow the European literature should note that *Erebia phellea* Philip & Troubridge (Troubridge & Philip, 1983. J.Res. Lep. 21:107-146) is a junior synonym of *Erebia occulta* Roos & Kimmich (1983. Ent. Z., Frankf.a.M. 93:69-77). Careful comparison of Roos & Kimmich's figures of genitalia and facies for *E. occulta* (TL 150 km Dempster Highway, Yukon Territory, Canada) with Yukon Territory specimens from the type series of *E. phellea* indicates that the two taxa are conspecific, and the publication date for *E. occulta* precedes that for *E. phellea* by four months. The TL for *E. phellea* is km 66-68 Council Road, Seward Peninsula, Alaska. This separation of type localities makes the specific epithet *phellea* available at the subspecies level if populations of *E. occulta* should later be differentiated as geographic races. The synonymy stands as follows:

Erebia occulta Roos & Kimmich, 1983.

Erebia phellea Philip & Troubridge, 1983. SYN. NOV.

The following citation does not form part of the synonymy, since no name was given, but it should be noted that:

Erebia new species B Ferris et al., (1983. Can. Ent. 115:823-840) is also a reference to *Erebia occulta*.

The Siberian range of *E. occulta* has been extended from that given in Troubridge & Philip (1983), where the only Siberian locality for the species was the Aborigen station of the Institute of Biological Problems of the North (Magadan), which lies on the eastern slope of Pik Vlastnyi, Bolshoy Annachag range, upper Kolyma valley, Magadanskaya Oblast'. In 1983 K. W. Philip and A. C. Jones found *E. occulta* (31 males, 2 females: 17-22 June) at the Rangifer field station of the Institute of Biological Problems of the North, which is situated in the upper Yama River valley, 26.5 km SSE of Atka (200 km southeast of the Aborigen station). The station, in the floodplain of a tributary of the Yama, is in larch taiga at 2500 feet (760 m) elevation, but most specimens of *E. occulta* were obtained on gravel scree from 2700-3400 feet (820-1040 m). A few specimens were captured on the valley floor, always on or near gravel or rocks. In addition, Philip was given a batch of material collected by I. Chereshnev on a low rocky hill at the mouth of the Cheutakan River, just east of Kresta Bay on the south coast of Chukotka, which contained a small series of *E. occulta* (8 males, 1 female: 7-9 July). Figure 1 illustrates the presently known range of *E. occulta* in the Magadanskaya Oblast', NE Siberia, U.S.S.R.

The Rangifer station and the Cheutakan River are separated by over 1600 km, in addition to having different biotopes: taiga at Rangifer and tundra at the Cheutakan River. It is not surprising that the facies of *E. occulta* from these two localities are somewhat different. The Rangifer specimens are larger (mean male FW length 22.4 ± 0.8 mm, N = 20), and the overall facies are close to material from the Aborigen station (see Troubridge & Philip, 1983). The Rangifer and Aborigen stations are both in the Okhotsk/Kolyma Uplands, and faunal similarity would be expected. Specimens from the Cheutakan River are appreciably smaller (mean male FW length 19.9 ± 0.9 mm, N = 8), and have facies intermediate between western Alaskan specimens and Okhotsk/Kolyma Uplands specimens. The black pupils of the DFW submarginal ocelli are larger than in Alaskan specimens (up to

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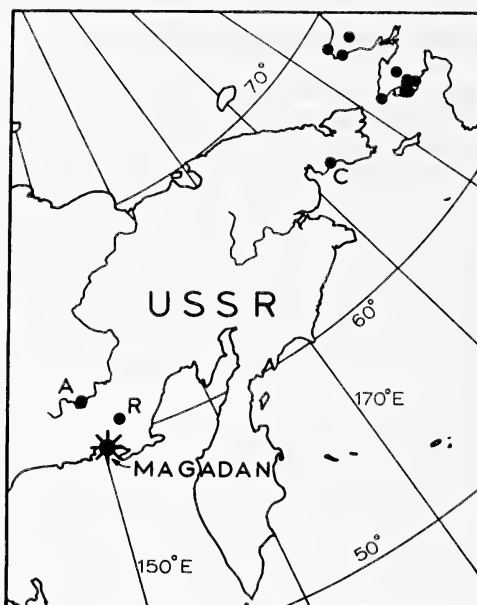
Fig. 1.   Range of *Erebia occulta* in the Magadanskaya Oblast'. **A:** Aborigen
field station, Bolshoy Annachag Range, upper Kolyma valley. **R:**
Rangifer field station, upper Yama River. **C:** mouth of Cheutakan River,
Chukotka. Distribution in western Alaska (unlabelled dots) is shown
as well.

1.0 mm wide, as in some Okhotsk/Kolyma Uplands specimens), but the VHW pattern has a distinct mesial band, and a noticeable speckling of lighter scales, which are both characteristic of western Alaskan specimens.

Alpine tundra areas near Markovo, on the Anadyr' River in Chukotka, were collected in July 1983, but no *E. occulta* were found. We thus have no information about this species in the regions between far eastern Chukotka and the Okhotsk/Kolyma Uplands, although *E. occulta* presumably flies in other parts of Chukotka.

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Weights and Dimensions of *Hyalophora euryalis* Pupae[1]
(Lepidoptera: Saturniidae)

The ceanothus silkmoth, *Hyalophora euryalis* (Boisduval) occurs in the United States along the Pacific coast (Collins & Weast, 1961; Ferguson, 1972). Mosher (1916) described the pupae of this species (under the name *Samia californica* Grote), but she gave only sparse dimensional information and did not discuss the genital openings or sex-related size differences. During November 1982, wild cocoons and 5th instars were collected at Presidio of Monterey, between Monterey and Pacific Grove, California. The food plant was Carmel creeper, *Ceanothus griseus* var. *horizontalis*. The ceanothus silkmoth is seldom locally abundant and, among saturniids, is particularly difficult to rear to obtain research specimens (Collins & Weast, 1961; Miller & Cooper, 1980). The availability of these wild specimens from the Presidio of Monterey provided an opportunity to examine the dimensional characteristics of this little studied species. After all individuals had pupated, they were removed from the cocoons and sexed according to the very distinct genital openings on the venter of the 8th and 9th abdominal segments. The genital openings in the ceanothus silkmoth are virtually identical in character to those described and illustrated by Miller et al. (1982) for *Hyalophora cecropia* (Linnaeus). Twelve ceanothus pupae of each sex were weighed and measured as described by Miller et al. (1982). The weights and dimensions are shown in Table 1.

Table 1. Weights and Dimensions of Wild Ceanothus Silkmoth Pupae.

Measurement	Males (n=12)			Females (n=12)		
	Mean		S.D.	Mean		S.D.
Weight	3.8	±	0.6	4.5	±	0.8
Length	32.8	±	2.4	34.2	±	2.2
Width	14.7	±	0.6	15.8	±	0.8
Circumference	44.1	±	1.9	47.4	±	2.7
Antenna Length	17.9	±	1.3	14.8	±	1.1
Antenna Width	8.1	±	0.5	4.7	±	0.5
Antenna Length to Width Ratio	2.2	±	0.2	3.2	±	0.3

weights in grams; dimensions in millimeters

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[1]The opinions contained herein are those of the author and should not be construed as official or reflecting the views of the Department of the Army.

An Early Season Migration of *Catopsilia pomona* (Lepidoptera: Pieridae) in Java, Indonesia

Catopsilia pomona (F.) is a well-known migrant in parts of Indonesia, and has been recorded many times migrating during the wet season in Java (C. B. Williams, 1930, The migration of butterflies. Edinburgh: Oliver and Boyd). However, as Yukawa (J. Yukawa, 1983, An observation on the migratory flights of *Catopsilia pomona pomona* (Fabricius) in Carita, Java. Tyo to Ga, 33:185-186) observed, there are no records of such flights from June to September, and the main migratory season corresponds with the commencement of the north-east monsoon from November onwards. This note is to record a migration of *C. pomona* in south-west Java in mid-September, providing a substantial addition to the known flight period of this species. Any definable insect migration in the Sunda Strait area is of potential importance in assessing likely colonisation patterns of the Krakatau group of islands, and it is of interest that occasional large pale pierids were seen on several of the islands earlier in September, but were not captured. It is possible that they represented the pale *crocale* Cr. form of *C. pomona*.

The present flight was observed on the west coast of the Ujung Kulon Peninsula, between Ciramea and Cikelappabeurrem, on the morning of September 20, 1984. Butterflies were moving from North to South, both along the beach and for several hundred m out to sea. They were observed over about two hours during which some 75 individuals were noted flying in the same direction and in an undistracted manner. At Ciramea, a ten minute observation period yielded 43 individuals crossing a defined beach transect, and the dense forest vegetation fringing the beach probably led to 'funneling' of the butterflies into this open area. Heights of flight were 1-3 m, with occasional higher individuals.

On both September 19 and 20, 1984, non-migratory individuals were seen feeding on blossom at Cankeuteuk, on the northern side of the Peninsula, and, although *C. pomona* was not seen on the nearby island Pulau Peucang during the previous week, individuals were observed there frequently from September 20-23, 1984, when observations stopped.

The morning of September 20, 1984, was fine, clear and sunny, but there had

been substantial rain accompanied by a westerly breeze on the previous day, as well as rain on several days during the previous week. This rain was regarded as unseasonal, and as an early extension of the normal 'wet season'. Both sexes of *C. pomona* were present and this apparently unseasonal migration was possibly associated with earlier than usual rain.

This note is a byproduct of the 1984 Zoological Expedition to the Krakataus (major sponsor Mr. Dick Smith of Australian Geographical Magazine). We thank Prof. I. W. B. Thornton for the opportunity to participate in the Expedition.

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A Range Extension and dark Phenotype of Hemileuca Chinatiensis

On October 15, 1980, while traveling north on Route 62 just south of Whites City, New Mexico, my wife and I noticed what we believed to be *Hemileuca chinatiensis* Tinkham flying across the highway. After collection of specimens and examination, we found some of them to be a very dark phenotype of *chinatiensis*, appearing somewhat as *H. juno* Packard. In all, 25 specimens were collected before the wind forced us to give up. Nearly 50% of the specimens were the dark phenotype. From the records I find this is a northern range extension of *chinatiensis*, which is described only from southwest Texas and Culbertson Co., Texas. The habitat in New Mexico is very similar to that found south of Marathon, Texas, where *chinatiensis* is abundant.

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Revisions to the Checklist of World Libytheidae

After I published a checklist to Libytheidae (*J. Res. Lepid.* 22:264-266, 1984), a few additions and changes surfaced.

Dr. Gerardo Lamas Muller (*in litt.*) notes that the family name Libytheidae Duponchel 1844 should be ascribed to Boisduval (1833, *Faune entomologique de Madagascar*, p. 52; cf. Cowan, 1979, *Ent. Rec.* 91(2/3):61-64, (6):146-149), and that *L. carinenta* Cramer was described in 1777, not 1779.

Mr. Kikumaro Okano (*in litt.*) also pointed out the Cramer date (Brown, 1941, *Ann. Ent. Soc. Amer.* 34:127-138) and has brought the following subspecies to my attention:

1. *L. geoffroy eborinus* Samson 1980—San Cristobal (Solomons).
2. *L. myrrha iwanagai* Hayashi 1976—Palawan.
3. *L. celtis yayeyamana* Fujioka 1975—Iriomote and Ishigaki (Yayeyama Islands). These islands should thus be deleted under *L. celtis formosana*.

Under *L. celtis amamiana*, add Okinawa, and delete this island for *L. celtis celtoides*. *L. narina neratia* Felder should read C. & R. Felder.

Distribution maps and data for Libytheidae will appear in a forthcoming zoogeographic study (*Tokurana*, in press).

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Three Intersubfamilial Matings in Nature (Lycaenidae)

Two mated pairs of field-collected Lycaenids, representing respectively an inter-subfamilial and intertribal pair, recently were acquired by the Los Angeles County Museum of Natural History. The first, collected by the late Chris Henne, involved a male *Apodemia mormo* and female *Brephidium exilis* at Big Rock Creek, San Gabriel Mountains, Los Angeles Co., California, 4000' on September 18, 1972. The specimens were preserved *in copula*, the male (*A. mormo*) pinned laterally with the female (*B. exilis*) supported by a paper triangle. The male genitalia completely engorge the distal quarter of the female. There is no question of the veracity of the mating, although we have no information of the circumstances of collection.

The second, male *Lycaena arota nubila* and female *Euphilotes battoides bernardino* were taken *in copula* and killed by cyanide gas, remaining coupled. The specimen was collected by Les Stockton along the Mulholland Highway in the Santa Monica Mountains, Los Angeles Co., California, at about 10 AM on May 31, 1981. Stockton reported the collection was accidental, the netting occurring during his attempt to take another butterfly. The mating pair just happened into the net. Except for a notation that the day was warm (c 30°C) and virtually windless, we have no further information. While awaiting curation at the museum, the specimen most unfortunately was destroyed by Dermestids.

Finally, R. A. Arnold (1984, Interim Report for Contract C-616, Calif. Dept. of Fish & Game) reported observing a paired male *Apodemia mormo virgulti* and female *Euphilotes battoides allyni* at the El Segundo Sand Dunes, Los Angeles Co., California, on July 18, 1984. The coupling lasted from 1232 to 1337 PDT. No further data were given and the specimens were not taken.

Pairings between individuals of generic or higher levels of differentiation are extremely uncommon, and, although spectacular, are probably of only trivial biological significance. The obvious questions raised by such matings include 1) how did the sequence of behavioral stimuli and responses break down, 2) were the mechanics of mating effective, resulting in transfer of spermatophore, in spite of the differences in both size and morphology, 3) could the female maintain sperm viability, 4) would the "genetic systems" be sufficiently compatible to provide viable or even fertile offspring?

The latter two questions, particularly the last, most likely have negative answers. I am not aware of any proported hybrids other than among closely related butterflies, where such hybrids, in fact, are recurrant and genetically meaningful (e.g. *Limenitis, Colias, Vanessa, Lycaena*, etc.). A positive answer to question, concerning the effectiveness of spermatophore transfer between distantly related species, bears on the value of genitalia as taxonomic characters. Previous comments on the subject made by Shapiro (1979, The Assumption of adaptivity in genital morphology, J. Res. Lep. 17:68-72) and Lorkovic's experiments showing that mutilation of male genitalia does not hinder interspecific matings (1955, Zavisnost Varijabilnosti Organa Muskoc Genitalog Aparata Kukaca Njihovoj Funklionalnoj Vrijednosti, Biol. Glasn. 7:234-235) are particularly pertinent. There are no clues concerning the first question, as we know little enough about normal intraspecific mating behavior in these butterflies.

All the above questions are amenable to experimental attack, however, because many Lycaenids mate in confinement and breed without the need of artificial pairing. Hence this butterfly family may be an especially effective group in which the

relative roles of pre- and postzygotic barriers to reproduction might be explored.

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A Melanic *Colias euxanthe stuebeli* **from Peru (Pieridae)**

Melanic male aberrations are known from a number of *Colias* species. They range from partial to complete on the dorsal surface but are rarely fully melanized ventrally. A melanic aberration of the male of *Colias euxanthe stuebeli* Reiss. was taken 6 July 1984 2 km E Catca, Department of Cusco, Peru, by S. P. Courtney and M. J. Stern. Approximately half the scales in the normally orange area (except the scent patches and near them) are black, producing a very distinctive appearance (Fig. 1). Remarkably, the underside is entirely normal. The "ventral median flush" of black scales on the forewing is heavy, but within the normal range of variation.

The U.S. National Museum contains five melanic male *Colias philodice* Latr. from the United States. One of these is fully blackened on both surfaces. The other four are roughly as melanized dorsally as the Catca specimen, but all display a black area on the ventral forewing which seems characteristic of melanic males in the Nearctic *Colias*. The absence of this marking on the Catca specimen suggests that the variation is probably not homologous.
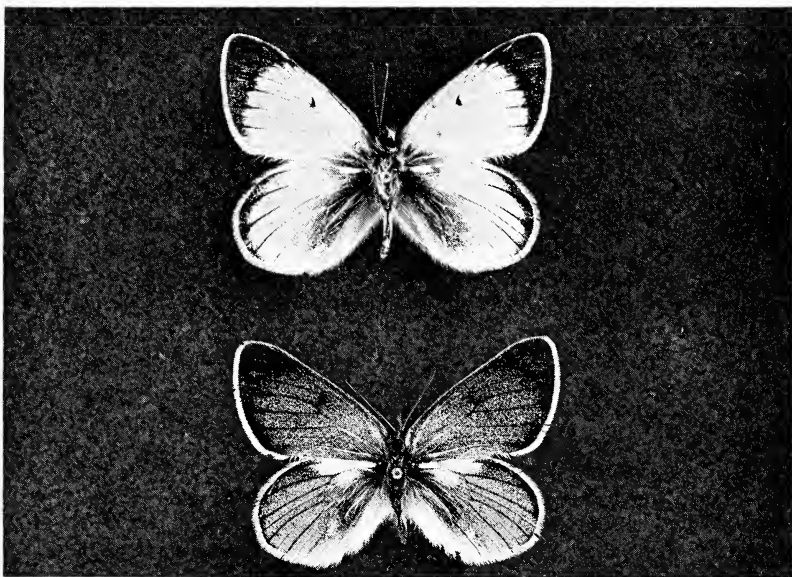

Fig. 1.   Dorsal surface of normal and melanic male *Colias euxanthe stuebeli* from Catca, Depto. Cusco, Peru, 6 July 1984.

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Book Reviews

Handbook of Moth Ecology.
Miyata, Akira, 1983. Showado Printing Publishing Division, Japan. 1451 pp. (in Japanese) in 2 volumes + 16 pp. English summary. No price stated.

In the sciences an English speaking person cannot be accused of chauvanism for balking at foreign language works, because English is the de facto language of science. It is consequently unfortunate that this very data rich and generally significant work does not have more of its content in English and thus be universally available.

Volume I lists 3370 moth species of Japan with their known foodplants, understandable by Latin nomenclature. Buried are details on habitat, phenology, nocturnal activity, diapause stage, and distribution. The second volume turns these data around and lists 1056 foodplants with their moth hosts. Then we have a biogeographical table with each species and its distribution by main islands, prefectures of Kyushu, and the islands of the Amami and Ryuku chains, each species classified by its general distribution outside Japan, and some distribution maps. Next is a section on methodology of collecting for quantative purposes, discussion on flight time activity and interrelation with climatic factors. Finally a biogeographical discussion highlighting habitat relationships, specifically with inter-island distributions. The English summary provides some guide to tables and figures which are not otherwise immediately obvious.

What is seriously missing is an understanding to just what the intriguing subtitle "Moths as an Indicator of the Environment" refers. Is there a hidden correlation of species clusters with modal ecological aggregates (biomes) or are we presented with an approach as Kudrna uses in his forthcoming *Butterflies of Europe* where Lepidoptera are viewed as important elements in assessing environmental quality? Either way this work appears too valuable to have been denied access by the greater scientific community.

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Advances and Challenges in Insect Rearing.
King, E. G. & N. C. Leppla, 1984. ARS/USDA, New Orleans. xvi + 306 pp. Price: $8.00 (U.S. Government Printing Office, Washington, D.C. 20402)

Although aimed primarily at those concerned with mass rearing of all insect groups for economic purposes, there is a wealth of theory and practical information in this volume for everyone involved in rearing any insects. The publication derives from a symposium on the subject. In the "How To" section, over half the procedures discussed concern Lepidoptera, which emphasize programs for mega individual production under factory conditions. Nevertheless the principles of rearing on artificial diets, genetic effects, disease problems, material resources, etc. make this a valuable reference and at the price a real bargain.

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Phenetics and Ecology of Hybridization in Buckeye Butterflies (Lepidoptera: Nymphalidae).
Hafernik, J. E., Jr. University of California Publications in Entomology, Volume 96, pp. 109. 1982.

In his great book *How to Become Extinct*, the late, lamented humorist Will Cuppy wrote: "The term *species*, in its application to fish, was first clearly defined by F. Willughby in his *Historia Piscium* (1686), and from that day to this the whole thing has been in a fearful muddle." Although Buckeyes are not fish, they might as well be; at least they are in a fearful muddle. There is enough in that muddle to generate at least ten Ph.D. theses. This is the first of them.

Hafernik defines his objectives in the Introduction. It is characteristic of scientific writing that work is always presented as rigorously logical, completely planned in a rational manner in advance—despite the serendipitous character of so much research, the blunders and false starts and lucky breaks we all know well. Thus, it appears from his own words that Hafernik was immensely successful at meeting his objectives. He was, in fact, reasonably successful in his attempt to apply the biological species concept to most (not all) of the North and Middle American *Junonia*. He did not, however, settle definitively the row begun by W. T. M. Forbes 55 years ago as to whether the Buckeyes represent a case of "circular overlap." That is a pity, because the concept is a classic challenge to the biological species definition, and there are very few good cases around. (*Pieris napi* and *bryoniae* in Europe *may* be one of them.)

The study entailed making many hybrid crosses and carrying them to the F_2 and backcrosses in order to quantify Oliver's compatibility parameters. Making crosses in Buckeyes is not like making crosses in Pierids. These animals do not mate readily in cages and cannot be hand-paired, and one has to use experienced wild males subjected to a bait-and-switch technique using chilled virgins. The technique is tedious; having used it myself I can say I would rather go to the dentist. The resulting adults were used as reference groups for discriminant-function analysis, for the analysis of the inheritance of phenotypic differences between taxa, and for field tests of the visual component of reproductive isolation. Discriminant analysis is a powerful tool in systematics and particularly in analyzing intergrading populations (cf. the forthcoming volume by M. M. Collins on *Hyalophora*, Saturniidae, in the same U.C. series), but its power is inherently limited by the insight of the investigator in selecting character systems and reference populations. In itself, it is powerless to distinguish between primary intergradation and the secondary kind, that is, hybridization. John Endler has argued on theoretical grounds that this distinction is *generally* very difficult or impossible. Hafernik does not really address this question, nor does he provide any historical scenario to account for the present distribution of the entities in *Junonia*. For the super-rigorous Popperians, failure to tell tales is praiseworthy; for those of us brought up on them, it is a let-down.

Hafernik arrives at twelve conclusions. They are a mixed lot, some on much firmer footing than others. Here they are, with comments.

1. "Phenotypic differences in color among North and Central American *Junonia* are probably not associated with major genomic reorganization, but are rather the result of allelic differences at a few loci." This is based on the remarkably high levels of genetic and developmental compatibility among the entities. It seems plain now

that reproductive isolation can occur based on changes in a minuscule portion of the genome (Hawaiian *Drosophila*) and that organisms which are phenotypically very different can be astonishingly similar genomically (man and the chimpanzee), so Hafernik's finding (not, by the way, including any biochemical genetics) is not all that surprising.

2. "Color pattern differences among females act as isolating mechanisms, with males courting females with color patterns similar to their own." O.K. as far as it goes. Unfortunately, no workable assay was found to quantitate *female* preference among *males* (we have seen that this is a very important component in *Colias* hybridization, for example), so only half the story has been told. (See also Shapiro, 1983, *Psyche* 90:59-65 for an experiment which corroborates Hafernik's conclusions while eliminating a potential methodological problem.)

3. "Pheromones may not be important for *Junonia* courtship. Males can recognize prospective mates by color pattern and flight pattern alone." Perhaps, but the potential role of pheromones has not been rigorously *excluded*.

4. "Reproductive isolation can arise from changes at one or a few loci controlling color patterns." When 1, 2 and 3 above are combined as premises in a classic syllogism, this is the logical conclusion.

5. "Although unlike phenotypes are courted infrequently, males are less discriminating in their choice of a mate during the late stages of courtship. This condition leads to hybridization." Perhaps; certainly plausible.

6. "Hybridization is largely restricted to areas where at least one species is common, and thus there are many opportunities for mistaken courtships." Better quantification of density-relatedness is desirable; it has proved to be a major factor in the *Colias* hybridization story.

7. "F₁ and backcrosses are highly fertile, and this may result in introgression. In South Texas, genes of *J. coenia* have apparently been incorporated into the gene pool of *J. nigrosuffusa*." Independent evidence, such as *might* be provided by electrophoresis, is desirable here; it might also help to test the inference that we are seeing secondary, not primary, intergradation.

8. "Individuals of *Junonia* are quite vagile and range widely. . .movements of individuals into areas of sympatry. . .from areas of allopatry probably retard selection for perfection of isolating mechanisms." No surprise here. The surprise is that the eminently logical model for reinforcement of reproductive isolating mechanisms in secondary sympatry, long a staple in our evolutionary diet, is now under attack and seems to stand on pitifully little *evidence*.

9. "Incomplete reproductive isolation may be a recent result of man's activities, which have produced large new habitats, more contiguous ranges, and larger population sizes." Could be (I argue the same way about the hybridizing Pierids of the genus *Tatochila* in NW Patagonia!), but, as usual, the documentation for such claims is, well, nonexistent.

10. "Phenetic studies show. . .typical *J. zonalis* and *J. nigrosuffusa*. . .should be considered conspecific and combined under *J. evarete. J. coenia* is a species that is broadly sympatric with and at least partially reproductively isolated from *J. evarete.*" By Hafernik's own statement, isolation between *nigrosuffusa* and *coenia* is nearly complete in southeastern Arizona, perhaps incomplete in Florida, and demonstrably incomplete in Texas. The Caribbean remains a black box. In short, we know a lot more than Forbes did, and yet it still seems that *coenia* and *evarete* are "almost" species, more so in some places than others. That is the price we pay for

believing that speciation is a *process*.

11. "*Junonia coenia* and *J. nigrosuffusa* have different oviposition and larval foodpant preferences in Texas." Unequivocally true; "habitat selection" might have been added, too.

12. "Larval foodplant preferences...in areas of sympatry are probably related to the effects of both competition and hybridization." Well, maybe, but as usual, references to competition in phytophagous insects are basically baloney: there is little evidence that it even *exists*, let alone being a major organizing force in communities.

So much for the first chapter in the unraveling of the Buckeye problem. Before summing up, let me—as a member of the Editorial Board of U.C. Publications in Entomology—put in a good word for "house organs." Far too many theses or other studies which form unified wholes are chopped up more or less arbitrarily to generate journal articles. *U.C. Pubs. in Ent.* offers an important outlet for work which should be kept together and which transcends the length limits of most journals. It is particularly attractive for biosystematic work. Its past record includes such classic revisionary work as MacNeill's on *Hesperia* and Burns' on *Erynnis*. Alas, the physical format of recent volumes is not so attractive as in the "old days," but efforts are being made to change that. Contributions to the U.C. series are refereed, both in- and out-of-house.

The Buckeyes are still a fearful muddle. Who out there is ready to take on the Caribbean basin populations?

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Butterflies East of the Great Plains: An Illustrated Natural History.
Opler, Paul A. and George O. Krizek, 1984. Johns Hopkins University Press, Baltimore and London. 294 pp. Price: $49.50.

This is *not* a field guide. In fact, it is not certain what it *is*, but whatever it is, it is outstanding.

Butterflies East of the Great Plains is a medium-large format book, 8 ¾" x 11 ¼", about the size of many college textbooks. Although there is no way it can fit in a pocket, it is in many ways the logical successor to A. B. Klots' *Field Guide to the Butterflies of North America, East of the Great Plains*. It covers the same well-worked yet constantly surprising fauna (but for the U.S. only). The introduction, by Jerry Powell, gives Klots the credit he so richly deserves for making the living butterfly the focus of our attention; it is thus somewhat annoying to see the jacket blurb praise the present book as "like no other...the first butterfly book ever to emphasize the butterfly as a living organism rather than a specimen." At any rate, the book is in a lineal tradition from William Henry Edwards and Samuel Hubbard Scudder through Alexander Barrett Klots, and that in itself is a strong recommendation.

Opler and Krizek do *update* Klots, incorporating a great deal of information accumulated since 1951 on biology, behavior, and especially host-plant relations and geographic distribution. These are not referenced as a rule—this is a popular, not a scholarly, treatise—but they are presented with some care, so that the

speculative and the dubious are not "validated" once again by citation. (My own 1966 record of a second brood of *Thymelicus lineola* is cited as exceptional on p. 225. In fact, it was almost surely an error based on an atypical late emergence—a matter I am pleased to set right.) Rather generalized range maps are presented for most species, with distant outliers given as dots. The range maps are mostly more detailed than any presented before, however. They are derived from the very ambitious mapping scheme developed by Opler in the context of his Fish and Wildlife Service work on endangered species, and combine published and museum data with an extensive correspondence. Many of them are extremely interesting, if not readily explicable. They should be of tremendous interest to plant geographers and others interested in Quaternary dispersal phenomena in eastern North America. The skipper data are especially rich: among them see particularly *Erynnis lucilius* (p. 214), *E. persius* (p. 215), *Pyrgus centaureae wyandot* (p. 215), *Hesperia ottoe* and *leonardus* (p. 228), *H. metea* (p. 229), *Atrytone arogos* (p. 240), *Poanes massasoit* (p. 243), *Problema byssus* (p. 242), *Atrytonopsis hianna* (p. 253), and *Amblyscirtes hegon* (p. 255). Are the disjunctions mapped here real, or artifacts of poor collecting or habitat destruction? Some of these maps potentially falsify hypotheses I advanced in my 1971 skipper-biogeography paper (J. Res. Lepid. 9:125-155, addenda 16:173-175), while others seem to sustain them. I hope there will be lively discussion in their wake, and a renaissance of interest in the much-maligned skippers, which in spite of their reputed difficulty of identification, are where most of the remaining "goodies" are in our eastern fauna.

There are 324 color photos. Most are by Krizek. According to the blurb all of them are of live and unstupefied animals—a sharp contrast to the *Audubon Society Field Guide*, which has all too many faked photos. (The only suspect ones in this book are figs. 49, 107, 119 and 216, all of which I will give the benefit of the doubt.) There are *no* misidentifications, and the locality of every photo is given in its caption, as is usually the identity of the plant the butterfly is on. There are no text-page references in the plates section—an unfortunate omission, but not as important as in a field guide. The color reproduction is excellent. The skipper section includes some very rare species and shots, but few readers would feel confident identifying species from them!

An unusual aspect of the book is Krizek's hobby of tracing the etymology (not entomology!) of butterfly names. This is given more or less haphazardly. The omissions do not seem to be predicated on difficulty: *mandan*, not explained, was the name of a major Indian tribal unit in the Great Plains. On the other hand, I have no idea what *pegala* means, who the Mitchell of Mitchell's Satyr was, or who the Carter was whose head was memorialized in *Carterocephalus*. I would love to know.

I found two matters of fact and one of judgment to argue with in this quite large book. (In the Audubon Society guide it averaged nearly one a page.) On p. 216 (map 206) the range of *Pyrgus communis* is shown in two tones of shading, indicating a core permanent range and a seasonal temporary one further north. As I stated in my New York faunal list, however, *communis* overwinters quite successfully every year in western and central New York. This in fact forms the basis for the authors' assertion that "midwestern populations may be more cold-tolerant than those found east of the Appalachians"—the upstate New York populations colonized from the west early in this century. The status of the upper midwest populations needs to be clarified. On p. 220 (map 210) the same criticism applies to the

treatment of *Nastra lherminier*. It is shown as only a temporary resident in SE Pennsylvania, southern New Jersey, and the New York City area. Based on nearly 20 years' experience, however, I can confirm my statement in *Butterflies of the Delaware Valley* (1966) that this species overwinters reliably on the Coastal Plain (but not upland) every year. I still do not understand the assertion that it is an immigrant. The matter of judgment concerns the treatment of *Euphyes dion* and *alabamae*, derived from a personal communication by John Burns: for once I think the Miller & Brown checklist may be correct in treating them as full species.

Ah, yes, the Miller & Brown list. Readers waiting with baited breath will be pleased to learn that Opler and Krizek are conservative at the generic level: most of the swallowtails are still *Papilio*, the coppers *Lycaena*. Since the specific epithets are up-to-date (the abominable *hyllus* for *thoe*, for example), we must assume the generic names used represent a conscious choice. And let us say, Amen.

The introductory matter includes thumbnail sketches of aspects of butterfly population biology and the techniques used for studying them (warning: do *not* use the marking system illustrated with a Buckeye in fig. 5, p. 7—the marks are too near the margin and very vulnerable to being lost by fraying or especially predator attack. What are those eye-spots for?). There is a well-deserved emphasis on phenology, a subject in which Opler has long held a major interest.

I have not yet found one typographical error in this book. I cannot say the same of any other book I have read this year.

Who will buy *Butterflies East of the Great Plains*? It has something for everyone with an interest in butterflies, and I recommend it heartily to all, price notwithstanding. Its mission is not clearly defined, but I think I see a special role for it. Buy it for a teenage Lepidopterist you know. It is at just the right level of sophistication to lead him or her into an appreciation of what the interesting scientific problems are. (If you are like me, you'll read the book before giving it away. You will then buy a second copy for yourself.)

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Butterflies of Saudi Arabia and its Neighbours.
Larsen, Torben B. Stacey International, London; 160 pp., incl. 23 colour plates, ill.; size ca. 22 x 29 cm.

The handsome book under review consists of two separate parts: (1) a general account of butterflies tailored to the needs of the Arabian environment and readers (but very useful outside that region), and (2) attractive colour plates featuring all species of Papilionoidea and Hesperiidae of the Arabian Peninsula, based on good colour photographs taken by the author (but, unfortunately, suffering from not entirely constant reproduction by the printers, if judged by stringent standards).

Topics dealt within the general part include such things as: What is a butterfly?; butterfly life cycles; Arabian butterflies; butterfly variation; butterfly structure; butterfly behaviour; butterfly migrations; where butterflies are found; enemies and defense; butterfly geography; butterflies as pests; conservation and collecting of butterflies.

The book can be judged from two different points of view: (1) as an independent publication, and (2) as a sister volume to Larsen's monograph of the butterflies of the Arabian Peninsula (cf. Fauna Saudi Arabia 5:333-478, 1983), which it fulfills admirably. If judged as an entirely self-contained publication, the book deserves both much praise and some critical remarks. The appreciation is for the knowledgeable insight into the biology of butterflies in arid regions, written in a most acceptable style, easy to understand and most pleasant to read; as well as for some very good colour photographs of live butterflies taken by the author during his numerous research visits to Arabia and neighbouring countries. The critique is for the distinct "gap" between the general part and the colour plates. It would have surely been most appropriate to bridge this "gap" by furnishing brief data on the distribution, biology and identification of all species figured in colour on the plates, as well as a simple key or guide to their identification. (As the author is certainly capable of fulfilling this task admirably, the recommendation should be given some though if the book ever comes to reissue).

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Wir bestimmen Schmetterlinge.
Manfred Koch, 1984, revised by W. Heinicke (1st edition). 792 pp., 16 + 24 + 24 + 20 col. pls., numerous, mostly unnumbered, line drawings. J. Neumann-Neudamm, Melsungen (a subsidiary of an East German publishing house, printed in E. Germany). Price DM 58.--.

Manfred Koch's identification guide to the Macrolepidoptera of the German Democratic Republic is an old, well known publication. It is relevant by and large to most of central Europe and includes notes on western German species (the Alps excluded). It is the only identification guide of its kind on the market, not only in the German language. The present edition has been extensively revised. In the present edition, all four slim volumes were joined together in one impressive book. The systematic part is arranged into four "subvolumes", each with the relevant colour plates and line drawings. The text is arranged in columns and provides information on the distribution, phenology, larval hostplants, abundance; and there are also additional remarks on the variation, identifications, diagnostic characters, genitalia as the authors felt fit to include. A single index of Latin and German names is at the end of the book. The colour plates are unfortunately unchanged with no improvement of the quality, and include adults and some selected larvae. The general part includes the following topics: introduction; glossary; nomenclature (which is not up-to-date); collecting (The methods are rather extensive and amusingly out of date. The gentleman illustrated on p. 46 represents the time of World War I as do the carbide or oil lamps which could now only be purchased from antique dealers.); breeding; spreading; preservation of collections; protection of species in Germany; lepidopterous pests; and preparation of genitalia. All in all, the publication of the book is positive. It is only a pity that more attention to detail and a modern approach are lacking.

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Checklist of the Lepidoptera North of Mexico.
Hodges, Ronald W. et al., 1983. E. W. Classey and the Wedge Entomological
Research Foundation. ISBN 086096-016-1, xxiv + 284 pp. Price: $88.00,
paperback.

What, after all, can one say about the appearance of new faunal lists or
catalogues, except to note that they have arrived. This particular monograph,
however, really is noteworthy as it stands as printed proof that not all inflation has
been brought under control in the last few years. Indeed, this recent volume in the
burgeoning *Moths of North America* series offers us inflation on two fronts.
    The first inflationary assault is in the form of yet another slightly adjusted ver-
sion of Miller and Brown's much discussed butterfly nomenclature (pp. 42-65).
This nomenclature, championed by but a handful, has rapidly invaded our
libraries—the butterfly portion of this work completing a nomenclatural trilogy of
sorts with *The Butterflies of the Rocky Mountain States* (Ferris and Brown, 1981,
University of Oklahoma Press) and *A Catalogue/Checklist of the Butterflies of
America North of Mexico* (Miller and Brown, 1981, Lep. Soc. Mem. No. 2).
Miller's avowed distaste for the use of subgenera (Miller and Brown, 1981, p. v) has
led to a decidedly uneven treatment in the subject of this review as in the two pre-
vious publications. A number of weakly differentiated species groups are raised to
the generic level (for instance those within *Euphydryas*) while arguably "better"
species groups (e.g., *Erynnides* within *Erynnis*) are not so treated.
    But the butterfly nomenclature presented curiously differs from Miller and
Brown's (1981) sibling treatment. A sampling of the more egregious fractioning of
genera has been rectified (although whether this list, in fact, preceded the 1981
checklist is not clear). *Papilio* and *Eurema*, for example, have been reconstituted.
Nonetheless, much unwarranted fragmenting of long-accepted genera remains.
This includes acceptance of biologically unjustified treatments at the species level
(e.g., recognizing the ethereal *Mitoura* species "rosneri", "barryi", and "byrnei"),
at the generic level (e.g., recognizing the extremely closely-related species groups
within *Lycaena*, "Chalceria", Hyllolycaena", and "Gaeides"), and at the family
level (in contrast, see most recently Ackery [Chapter 1 in *The Biology of Butter-
flies*, 1984, Academic Press] for a balanced treatment consistent with available
evidence). And, since this treatment lacks the notes, dates, and other information
of the previous Miller and Brown (1981) butterfly list, this one is effectively
worthless.
    I hardly would venture to critique the taxonomic treatments for the moths which
comprise the bulk of this catalogue, but, at the very least, the contributing authors
are a first rate lot. The most recent inclusive checklist of the North American
moths (McDunnough, 1938, Mem. So. Cal. Acad. Sci., Vol. 1) was nearing its
golden anniversary, thus an updating certainly was necessary. But, while moth
specialists need not wade through the morass of rather mystical treatments that
face butterfly taxonomists, understanding of the basic structure of the moth com-
ponent of ditrysian relationships is still very much in flux indeed (as one can see in
interesting introductory remarks on the Pyralidae, p. xvii, and Geometridae, p.
xviii, and, for example in the placement of the genus *Ellabella* in no less than five
separate families by various workers, Heppner, 1984, J. Res. Lepid. 23:50-73).
That is not to suggest that all energies have been diverted to higher taxonomic

placement for the moths and that the moth arena is free of nomenclatural fisti-cuffs. The editor of this checklist himself has spoken to taxonomic inflation in the moths, in what might be expected to be the last frontier, the Microlepidoptera (Hodges, 1982, J. Lepid. Soc. 36:216-217).

Now, none of the aforementioned nomenclatural inflation necessarily makes a real case, pro or con, for this book; however the other, real dollars and cents infla-tion, certainly does. No, this is not a typo. That's right, eighty-eight dollars. . .for 284 pages. Almost a hundred bucks for a paperback—no text, no figures, no tables—just a list. Well, not *just* a list, in the sense that this is an important work-ing document to which all lepidopterists *should* have access. At this price they simply will not.

And we thought twenty-five dollars was a bit rugged for the initial offering in this series—158 pages plus plates on the Sphingidae! The stratospheric price for this list of Lepidoptera causes a recurrence of what is known as the "D'Abrera Effect", which was the result of having to scrape oneself off the floor after realizing that forty dollars got you 417 pages of Australian Region butterflies in 1977, and one hundred forty dollars gets you 244 pages of Oriental Region butterflies today. These are hardly isolated cases—try *The Genus Agrias: A Taxonomic and Illus-trated Guide* (Barselou, 1983, E. W. Classey), 96 pages for $57.50, *The Large White Butterfly* (Feltwell, 1981, Junk Pubs.), 542 pages (virtually all text) for $98.00, perhaps *A Monograph of the Birdwing Butterflies* (Haugum and Low, 1979), 277 pages (paper!) for $100.00. . .or the ultimate deal, LeMoult and Real (1962, E. W. Classey) on *Les Morphos*, about three hundred pages plus plates (mostly black and white), paperback, only $250.00.

Publishers have made a clear decision, and the decision does not include us. Sell several hundred atrociously over-priced copies of a checklist to the institutions that must have it and to the very few individuals that can afford it, versus the very real option of halving the price and more than doubling the sales of what would still be a grossly over-priced book. But they don't give a damn about us. Which is why my advice is straightforward. Don't buy this thing. Short of putting myself in con-spiracy of copyright violation, I suggest that you know how to get this book. It will run you about fifteen dollars and you can bind it to coordinate with your sofa. And if you feel guilty, you can leave the "Do not remove under penalty of law" tag on the matching eiderdown pillow you bought with all the money you saved. Let us hope they get the message.

Dennis D. Murphy, Department of Biological Sciences, Stanford University, Stanford, California 94305

INSTRUCTIONS TO AUTHORS

Manuscript Format: Two copies *must* be submitted (xeroxed or carbon papered), double-spaced, typed, on 8½ x 11 inch paper with wide margins. Number all pages consecutively and put author's name at top right corner of each page. If your typewriter does not have italic type, underline all words where italics are intended. Footnotes, although discouraged, must be typed on a separate sheet. Do not hyphenate words at the right margin. All **measurements** must be metric, with the exception of altitudes and distances which should include metric equivalents in parenthesis. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as example: 4. IV. 1979 (day-arabic numberal; month-Roman numeral; year-arabic numeral). Numerals must be used before measurements (5mm) or otherwise up to number ten e.g. (nine butterflies, 12 moths).

Title Page: All papers must have the title , author's name, author's address, and any titular reference and institutional approval reference, all on a separate title page. A **family citation must** be given in parenthesis (Lepidoptera: Hesperiidae) for referencing.

Abstracts and Short Papers: All papers exceeding two typed pages must be accompanied by an abstract of no more than 300 words. An additional summary is not required.

Name Citations and Systematic Works: The first mention of any organism should include the full scientific name with author (not abbreviated) and year of description. New descriptions should conform to the format: male: female, type data, diagnosis, distribution, discussion. There **must** be conformity to the current International Code of Zoological Nomenclature. We strongly urge deposition of types in major museums, all type depositions must be cited.

References: All citations in the text must be alphabetically listed under Literature Cited in the format given in recent issues. Abbrevations must conform to the *World List of Scientific Periodicals.* Do not underline periodicals. If four or less references are cited, please cite in body of text not in Literature Cited.

Tables: Tables should be minimized. Where used, they should be formulated to a size which will reduce to 4 x 6½ inches. Each table should be prepared as a line drawing or typed with heading and explanation on top and footnotes below. Number with Arabic numerals. Both horizontal and vertical rules may be indicated. Complex tables may be reproduced from typescript.

Illustrations: Color must be submitted as a transparency (i.e., slide) ONLY, the quality of which is critical. On request, the editor will supply separate detailed instructions for making the most suitable photographic ilustrations. Black and white photographs should be submitted on glossy paper, and, as with line drawings, must be mounted on stiff white cardboard. Authors **must** plan on illustrations for reduction to the 4 x 6½" page. Allowance should be made for legends beneath, unless many consecutive pages are used. Drawings should be in India ink at least twice the final size. Include a metric scale or calculate and state the actual magnification of each illustration as printed. Each figure should be cited and explained as such. The term "plate" should not be used. Each illustration should be identified as to author and title on the back, and should indicate whether the illustration be returned.

Legends should be separately typed on pages entitled "Explanation of Figures". Number legends consecutively with separate paragraph for each page of illustrations. Do not attach to illustrations. Retain original illustrations until paper finally accepted.

Review: All papers will be read by the editor(s) & submitted for formal review to two referees. Authors are welcome to suggest reviewers, and if received, submit name & comments of reviewers.

THE JOURNAL OF RESEARCH

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IN THIS ISSUE

COVER ILLUSTRATION: Fifth instar larva of *Caligo memnon* from a forthcoming paper by Allen Young to appear in Volume 24, Number 2.

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STATEMENT OF OWNERSHIP AND MANAGEMENT

Invited Paper

Measuring the Size of Lepidopteran Populations

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Introduction

When out in the field, do you often ask: "how many individuals of this butterfly or moth species are present here?" This number, the population size, is of great interest to the casual observer, collector, and research biologist alike (for different reasons)—but the simplicity of your question is deceptive. More often than not, a satisfactory numerical answer is difficult to obtain. The field of mark, release, and recapture (MRR) has developed to provide answers to such questions about animal abundance.

This paper is a largely non-technical synopsis of MRR theory and practice as usually applied to Lepidoptera. I will first describe several common MRR models, including the assumptions and the formulae with which each calculates population size; I then cover how they are put to practice, some associated pitfalls in interpretation, and the relative merits of the different models. Mark-recapture models estimate *absolute* abundance i.e., the actual number of individuals present. Because (1) absolute estimates may not be one's primary interest, and (2) conducting a mark-recapture study on a butterfly or moth population can be a time consuming venture, or even impossible, I will also discuss some simpler non-marking techniques for estimating *relative* abundance.

For the novice and sophisticated reader alike, I highly recommend Begon's (1979) little paperback, *Investigating Animal Abundance*, as a precis on mark-recapture. He presents the principles lucidly, and offers some of the best available advice for data analysis and interpretation. Blower et al.'s (1981) book is another good introductory reference. For the detailed statistical properties of MRR models, consult the treatises by Seber (1973) and especially Cormack (1968, 1979).

ABSOLUTE ABUNDANCE MODELS

Marking

To use most MRR models one must assign at minimum a *date-specific* mark to each captured animal. The main exception is the Lincoln Index

(and its derivatives), in which there is a single marking period, and
animals thus must only be classifiable upon later recapture as either
marked or unmarked. Nevertheless, it is always best to assign a *unique
mark* to each individual, because other factors (e.g., flight distances and
speeds) are hard to quantify unless one can recognize individual
animals.

How does one mark butterflies and moths? In virtually all cases, the
simplest mark to apply will be a number. Even with species having small
wingspans, a unique number can be written directly on one or more wings
(usually the basal underside) using fast-drying, permanent ink; "Shar-
pie" felt-tip pens or their equivalent serve admirably. For species with
variegated wing patterns, Ehrlich and Davidson's (1960) "1-2-4-7" sys-
tem or its modification (Brussard, 1970) can be used; Southwood (1978)
summarizes the diversity of other available marking methods and coding
schemes. For lepidopteran work in general, I advise against codes, for two
reasons: (1) numbers are simpler to write and remember; (2) codes are
very easily misread. Other aspects of the marking process are treated
elsewhere in this paper.

Principles

All absolute abundance MRR models share a common array of
assumptions, and most models also make additional ones. These
assumptions are interrelated, and encompass the many subtle aspects of
physical and temporal patterns of sampling, and the behavior of the
animals themselves. The major ones are:
  1) sampling is done in discrete intervals, that are short in relation to
     the total time of the study
  2) marked animals do not lose their marks
  3) marked animals can be distinguished from unmarked ones
  4) once marked, the behavior (*sensu lato*) of animals does not
     change
  5) marked animals mix thoroughly with the unmarked animals
  6) marked and unmarked animals have the same probability of
     capture
  7) sampling is random with respect to mark status (i.e., sexes, age
     classes, etc. are sampled at their natural proportions)
How to deal with these assumptions is covered in greater depth later.

I discuss four absolute abundance MRR models in this section: the Lin-
coln Index, Fisher-Ford, Jolly-Seber, and Manly-Parr models. These and
other models can be categorized broadly as either "single-marking" or
"multiple-marking" models. Single-marking models consist of one sample
during which marking and release are conducted, followed by one or more
samples in which animals are recaptured (the Lincoln Index is a single-
marking model). Multiple-marking models consist of a series of sampling

periods, during each of which marking, release, and recapture are conducted (Fisher-Ford, Manly-Parr, and Jolly-Seber are multiple-marking models).

The Lincoln Index, Fisher-Ford, Jolly-Seber, and Manly-Parr models determine population size using *ratios of marked to unmarked individuals*. The basic sampling principle is easily illustrated. Imagine a large box filled with ping-pong balls. A sample of balls is taken from the box, and each is marked with a stripe. The striped balls are returned to the box, which is then shaken vigorously. A second sample of balls is now drawn, which (in all likelihood) will contain some striped balls. The estimate of the total number of balls in the box then is: the number of balls in the first sample divided by the proportion of striped balls in the second sample (exactly so for the Lincoln Index—the three other models use only subtly different ratios to determine the total).

Single-Marking Models: the Lincoln Index

The Lincoln Index, or Peterson Estimator, is probably the most familiar of all absolute abundance models, and is the simplest and oldest of those described in this paper. Only two samples are necessary to obtain a Lincoln Index: a marking and recapture sample. The ping-pong example above calculated a simple Lincoln Index. In general, with:

n_1 = number of animals marked and released in first sample
n_2 = number of animals captured in the second sample
m = number of marked animals in the second sample
$\hat{N}$ = total population size

$$\hat{N} = \frac{n_1 \, n_2}{m} \quad \text{with} \quad \text{VAR} \, \hat{N} = \frac{n_1 \, n_2 \, (n_2 - m)}{m}$$

Bailey (1951, 1952) showed that this form of the Lincoln Index has a positive bias of the order $1/m$, and proposed the following continuity correction:

$$\hat{N} = \frac{n_1 \, (n_2 + 1)}{m + 1} \quad \text{with} \quad \text{VAR} \, \hat{N} = \frac{n_1 \, (n_2 + 1) \, (n_2 - m)}{(m + 1) \, (m + 2)}$$

Estimates of population size using either this or the first formulation differ only slightly unless sample sizes are very small.

Peterson, in 1889, and Lincoln, in 1930, are usually cited as the first to use the method. Bailey (1952) and LeCren (1965) both noted that Peterson apparently used his fish recaptures just to calculate mortality rates, and Lincoln's waterfowl study thus has priority in actual application of the model logic for estimating population size. However, LeCren (1965) also pointed out that Dahl used the principle in his 1917 studies of trout, and Cormack (1968) credits Sir Francis Bacon with similar reasoning several centuries earlier still. Because the method is so intuitive, there is

no doubt it has been independently discovered many other times.

The advantage of the Lincoln Index is its ease of calculation. Its disadvantage is an additional assumption, which rarely if ever will hold for the majority of lepidopteran populations:

8) the population suffers no gains or losses during the sampling interval.

Gains include birth (recruitment) and immigration; losses include mortality and emigration. Assumption eight thus addresses the concept of *population closure*. Actually, a population need not be truly closed to use the Lincoln Index: the model can be applied if there is neither recruitment nor immigration (which affect the number of unmarked animals), and if mortality and emigration also affect the marked and unmarked animals equally. Alternatively, one can make independent estimates of gains and losses, and account for them during data analysis (appropriately modified formulations of the Lincoln Index are discussed by Seber, 1973; and Begon, 1979, describes a weighted-mean version of the Lincoln Index for use with several days' recapture data). The Schnabel census and Jackson's "positive method" (see Cormack, 1979) are also essentially Lincoln Index models, the former being multiple-marking, the latter single-marking.

Multiple-Marking Models

The Fisher-Ford, Manly-Parr, and Jolly-Seber models all offer significant improvement over the Lincoln Index, by accounting for some or all of the sources of population gains and losses. Assumption eight is thereby relaxed. These three models require a series of censuses to determine gains and losses. Because previously marked animals are recaptured (and possibly remarked) on the second and later samples, multiple-marking models assume that:

9) the probability of recapture is unaffected by the number of previous captures (simply an extension of assumptions four and six).

FISHER-FORD

The Fisher-Ford model (Dowdeswell et al., 1940), Schnabel census, and Jackson's "negative method" are all early contemporary multiple-marking models. Fisher-Ford is sometimes referred to as a "trellis" model, for the manner in which the raw data are set up to do the calculations. Using terms as before, and with:

$\emptyset$ = residence rate over the period i to t (probability that an animal present at time i will be present at time t)

r = recaptures at time t of animals marked at time i

and: $\hat{N} = \dfrac{n_t\, m_i\, \emptyset}{r}$

(The symbol Ø is often referred to as the survival rate, but the term residence is more appropriate, since in practice death and emigration can usually not be separated from one another as sources of population loss). A *constant* residence rate which empirically best fits the data is first found by trial and error (procedure outlined by Fisher and Ford, 1947; and Begon, 1979). This rate is then used to determine the necessary Ø s.

A particular advantage of the Fisher-Ford model is that other variables e.g., catch rate, or periodicities in animal activity, can be incorporated easily into the model structure (Seber, 1973; Southwood, 1978). The (debatable) disadvantage is the assumption of a constant residence rate throughout the course of the study (see below). Bailey's (1952) Triple-Catch is a special three-sample case of the Fisher-Ford model.

JOLLY-SEBER

The Fisher-Ford model and its contemporaries are *deterministic*—one or more parameters are invariant. For example, an individual's chance of surviving from one sample to the next is assumed in Fisher-Ford to be an exact value, rather than a probability. Both the Jolly-Seber and Manly-Parr models are *stochastic*—the model parameters represent probabilities. Jolly (1965) and Seber (1965) independently derived stochastic models for open populations, although Jolly's differs by allowing for removal of captured animals from the population, an important consideration with Lepidoptera. In the terms of Jolly (1965), let:

n_i = number of animals captured in the ith sample
m_i = number of previously marked animals in the ith sample
s_i = number released from the ith sample after marking
r_i = number of the s_i which are caught subsequently
z_i = number of animals marked before time i which are *not* caught in the ith sample, but which *are* caught subsequently

$$\hat{N}_i = \frac{\hat{M}_i\, n_i}{m_i} \quad \hat{M}_i = m_i + \frac{s_i z_i}{r_i} : \quad \hat{N}_i = n_i + \frac{n_i s_i z_i}{m_i r_i}$$

$\hat{M}_i$ is an estimate of the total number of marked animals "at risk" of capture in the population at time i. The variance formula is:

$$\text{VAR}_{\hat{N}_i} = \hat{N}_i(\hat{N}_i - n_i)\left[\frac{\hat{M}_i - m_i + s_i}{\hat{M}_i}\left(\frac{1}{r_i} + \frac{1}{s_i}\right) + \left(\frac{1}{m_i} - \frac{1}{n_i}\right) \right]$$

The advantage of the Jolly-Seber model over the previous models is that it is fully stochastic, and can account for the usual sources of population gains and losses. It requires at least three samples, and makes an added assumption:

10) the probability of surviving from one sample to the next is the same

for each marked animal (i.e., age-independent residence)

The Jolly-Seber model has been criticized because it requires many parameters to be estimated, and is thus not parsimonious (Cormack, 1979). Various authors have also expressed the need for a stochastic model which assumes a (biologically often justifiable) constant residence rate, as with Fisher-Ford. Accordingly, Jolly (1982) recently developed three modified versions of the original Jolly-Seber model, covering the situations where residence rate, probability of capture, and both parameters are constant over time. Following Seber (1973), Jolly (1982) also adopted the following continuity correction for the original 1965 model, as per Bailey's (1952) modification of the Lincoln Index:

$$\hat{N}_i = \frac{\hat{M}_i n_i}{m_i} \quad \hat{M}_i = m_i + \frac{(s_i + 1) z_i}{(r_i + 1)}: \quad \hat{N}_i = n_i + \frac{(n_i + 1)(s_i + 1) z_i}{(m_i + 1)(r_i + 1)}$$

MANLY-PARR

Manly and Parr (1968) noted that with short-lived, discrete generation insects the age of animals marked first on day i is likely to be less than that of animals marked before day i. Because of the concomitant possibility of age-dependent mortality, and hence violation of assumption ten above, Manly and Parr developed a model based on sampling intensity—$n_i/\hat{N}_i$—a measure of the fraction of the resident population processed on a sampling occasion. The best available estimate of sampling intensity is $m_i/\hat{M}_i$, which can be calculated by setting up an individual mark table. For each day i, assign to an animal one of the symbols:

x = if this is its first or last capture
y = if this is an intermediate capture
z = if it is *not* captured, but *is* known to be present

Then, for any day i, the estimated sampling intensity will be the number of marked animals captured on day i divided by the number known to be present before and after, thus:

$$\hat{N}_i = \frac{n_i}{p_i} \quad \text{where sampling intensity, } p_i = \frac{m_i}{\hat{M}_i} = \frac{\Sigma y_i}{\Sigma y_i + \Sigma z_i}$$

$$\text{or:} \quad \hat{N}_i = \frac{n_i (\Sigma y_i + \Sigma z_i)}{\Sigma y_i}$$

The Manly-Parr model relaxes the assumption about mortality being independent of age. Its disadvantage is that it requires a high sampling intensity; Manly and Parr felt that y_i should exceed 10 for the method to be considered reliable.

Other Absolute Abundance Models

FREQUENCY-OF-CAPTURE

Some absolute abundance MRR models are not based on ratios of marked to unmarked individuals. Perhaps the best known are the "frequency-of-capture" models, which rely upon the distribution of different recapture classes: i.e., the number of animals caught once; number caught twice; thrice; and so forth. The "zero class" is the number of animals never caught, and the sum of all classes is the total population size. Various truncated discrete probability distributions have been fitted to the observed distributions of recapture classes, including the binomial, Poisson, and geometric distributions (see Seber, 1973, and Caughley, 1977).

Craig (1953) developed a frequency-of-capture model specifically with butterflies in mind. With the following terms:

x   = number of times an individual has been marked
f   = number of individuals that have been caught x times
Σ xf= total number of capture events (1 times number caught once, plus 2 times number caught twice, and so forth)

$$\text{and:} \quad \hat{N} = \frac{(\Sigma xf)^2}{\Sigma x^2 f - \Sigma xf}$$

Another method employing the same terms is that of Edwards and Eberhardt (1967), who used their model to measure cottontail abundance:

$$\hat{N} = \frac{\Sigma f}{1 - (\Sigma f / \Sigma xf)}$$

Frequency-of-capture models are often applied in a single-marking fashion, with one marking census and several recapture censuses (as per Edwards and Eberhardt, 1967). With highly mobile animals, these census periods can in principle be collapsed. The attraction that frequency-of-capture models thus have for work with Lepidoptera is that an absolute population estimate can be provided for a very brief time period—a day, or even less (Craig, 1953, envisioned a one day census). Problems with compressing the sampling interval are pursued to some extent later; essentially, immediately upon release, one must presume that marked animals are (1) catchable again, and (2) have mixed back into the population. The analogy is marking single ping-pong balls from the box described earlier, being able to shake the box vigorously enough in a second or so to mix all the balls, and repeating the sampling procedure many times for, say, an hour.

REMOVAL

Seber (1973), Caughley (1977) and Southwood (1978) all review models which rely upon removing segments of the population to estimate population size. The simplest technique is, on each of several sampling occasions, to capture a series of animals and *not* release them back into the population. The rate at which successive sample sizes drop off is proportional to the total population size and the number removed. The number of animals removed on the ith sample can be plotted (y-axis) against the sum of animals removed before the ith sample (x-axis), and the total population size (x-intercept) determined by linear regression.

A variant of this approach is to employ the ratios of "natural marks" in a population e.g., males and females, or polymorphs. The proportions of the natural marks are determined in a prior survey, and then removal sampling on one of the mark classes is carried out. The change in ratio of the natural marks from the first sample to the second is related to the total population size. This is Kelker's (1940) "change-in-ratio" method:

x = mark class from which individuals are removed

y = mark class not removed

n = *number* of the x that are removed

p = *proportion* of mark class i in population at time j

$$\hat{N} = n \left[p_{x1} - \frac{p_{y1}\, p_{x2}}{p_{y2}} \right]^{-1}$$

Dealing with the Assumptions

Failure to meet one or more assumptions made by a MRR model leads to predictably negative results. If one is unaware of violations, then there will more than likely be serious errors in interpretation. If one knows of the violations, then how one *tempers* data interpretation is the primary concern (it should go without saying that if assumptions are violated, one must not interpret results as if they held). One can often make appropriate allowances for violated assumptions when calculating populational parameters.

It is worth briefly listing the effects that violating three assumptions have on estimates of population size. Complete discussion of all aspects of MRR assumptions are given by Cormack (1979) and Begon (1979; Chapters 3-4). The three assumptions treated here are composites of the ten enumerated earlier; in practice, these three will also likely be confounded.

MARKING DOES NOT ALTER SUBSEQUENT ACTIVITY

A principal assumption of all but removal models is that marking does

not alter patterns of activity. Marking may either diminish an individual's chance of subsequent capture ("trap-shyness") or enhance its likelihood ("trap-happiness"); and with social animals, marking may even influence the unmarked members of the population.

If the marking process decreases the probability of recapture, then the number of marked animals in subsequent samples will be underrepresented, and $\hat{N}_i$ accordingly overestimated. If marked animals are more likely to be captured later, the converse is true. In *open* populations, $\hat{N}_i$ is unaffected if marking alters the probability of survival (perhaps a counterintuitive result). In *closed* populations, a decrease in survival probability leads to an overestimate in $\hat{N}_i$; conversely with an increase in survival probability.

One of the few times a removal model has an advantage over other MRR models is when marking *does* influence activity (the other time is as an alternative to frequency-of-capture models during a single census). Since there are no releases using removal methods, one is free from the assumption that marking has no effect. Removal sampling of Lepidoptera can be carried out non-destructively by accumulating all captured individuals in a flight cage until all sampling is complete, at which point releases are made. However, except during quite restricted instances, removal models will be inferior to the other MRR models. I pursue the assumption that marking does not alter behavior again in the context of comparing absolute and relative abundance models.

THE POPULATION IS CLOSED

Closure implies that there are neither gains (births, immigrations) nor losses (deaths, emigrations). The Lincoln Index and frequency-of-capture models assume population closure. When both gains and losses occur, the number of marked animals is being diluted over time. Overestimates of $\hat{N}_i$ will thereby occur when using these models. The same result can be expected when there are only gains to the population. If, however, there are only losses, *and* these occur in similar frequency in both the marked and unmarked fractions of the population, then $\hat{N}_i$ remains unaffected.

Implicit in the concept of closure is that emigration is permanent. If an animal emigrates from a population but returns again much later, then in practice it has been "trap-shy," as with an animal whose probability of recapture was decreased by marking. The effects on $\hat{N}_i$ estimates are then the same as those described in the preceding section.

ALL INDIVIDUALS ARE EQUALLY CATCHABLE

Most models assume that all animals in a population have the same catchability. There are many instances where catchabilities might differ: for example, inactive individuals are less likely to be captured than active

ones; and dominant individuals may be more visible than subordinate ones.

Should certain individuals be consistently more catchable than others, then the population size will be underestimated. If, however, the catchability differences are not consistent from census to census, the $\hat{N}$s will remain largely unaffected. A common situation is systematic differences in catchability among the sexes, or age classes; population size will tend to be underestimated in such instances.

"Probability of recapture" and "catchability" are potentially confusable terms. Strictly, at time i, the probability of recapture is the product of catchability (p_i) times residence ($\emptyset_i$). Because these two biologically distinct factors can mask one another, differences in recapture probability must be interpreted with caution. Working with *Colias* butterflies, Tabashnik (1980) developed new methods for disentangling these two elements of recapture probability; I have also explored the usefulness of these tests using data from *Boloria* (Gall, 1984a, 1984b). Because Tabashnik's methods for partitioning the components of recapture probability offer improvement over earlier ones (see Begon, 1979), I feel that his two tests should be incorporated as a matter of course into mark-recapture studies. Interested readers should consult Tabashnik (1980) for details; Carothers (1973) is another most illuminating paper that treats the catchability of taxi-cabs.

Utility of the Different Models

I have noted one or several circumstances in which each MRR model may be considered particularly appropriate. How do these models perform when pitted against each other? When making such comparisons, it is important to bear in mind that each model is designed for particular circumstances (hence the variation in assumptions). The performance of any model therefore is strongly study-dependent; different organisms and situations may define mutually exclusive sets of models as choices. For example, when a population suffers losses and gains, one would not select the simple Lincoln Index or a frequency-of-capture model, because these depend upon closure. Such models are designed for other situations. Whenever possible, though, one should compare results from an array of different MRR models, even if one or more of the models appears less appropriate *a priori*, because comparison provides crucial insight into the processes operant in the population, and helps clarify model applicability.

The Fisher-Ford, Manly-Parr, and Jolly-Seber models are considered to have the broadest applicability among available MRR models. The 1965 Jolly-Seber model is also currently touted as the brand leader among them, evidence having accumulated now from simulation studies, field work, and combined approaches (e.g., Manly, 1970; Bishop and Shep-

pard, 1973; Roff, 1973; Cormack, 1979; Begon, 1979; and references therein). Jolly's (1982) revised model, allowing for constant residence rate and/or probability of capture, will no doubt prove more broadly applicable still (few studies using the new formulations have yet been reported). These are vigorous endorsements for the Jolly model, but the salient points to remember in comparison are: Fisher-Ford assumes the most but requires the least data; Manly-Parr assumes the least but requires the highest sampling intesities; Jolly-Seber is intermediate on both counts. Begon (1979, pp. 53-54) summarizes:

> "If the data are sparse, and survival-rate both constant and age-independent, then Fisher-Ford is obviously the most applicable method. If the data are extensive, and survival-rate both variable and age-dependent, then Manly-Parr is appropriate. But there will be many situations in which the pros and cons are shared more evenly. It should be noted, for instance, that the more restrictive models are both fairly robust when their assumptions are violated. Thus, Jolly is preferable to Fisher-Ford only if survival-rate varies *significantly*, and Manly-Parr preferable to Jolly only if survival is *strongly* age-dependent."

I stress the distinction between concluding that a model is more applicable, and concluding that it is in some intrinsic sense "better" than others. Because model performance depends upon context, the latter conclusion does not necessarily follow.

RELATIVE ABUNDANCE MODELS

There are at least three cogent reasons why one might opt *not* to conduct a mark-recapture program to assess the abundance of a particular species. First, the cost of gathering such data is high. One typically must invest a large amount of energy in both field work and analysis time to carry out an MRR stiudy. Second, it may be impossible to conduct an MRR study: individuals may fly at the tops of trees; netting specimens may not be allowed; and so forth. Third, *absolute* abundance may not be of primary interest. The investigator may be asking: how has the size of the butterfly population in my backyard varied over the past ten years? Such a question deals with *relative trends* in abundance, and does not strictly require that absolute numbers be known.

Overview

Most techniques for measuring relative abundance are simple, requiring a minimum of investigator effort and equipment. Arrays of relative methods are documented in the literature, many having been conceived for a single species (and/or out of necessity, because applying an absolute abundance model would have been out of the question). These span the range from listening for animals, through direct counts and transect

sampling, to both passive and mobile traps; and also include methods based not on the animals themselves, but on by-products such as feces or extent of defoliation (see Doane and McManus, 1981, for examples of the use of by-products as indices of lepidopteran populations). Southwood (1978) provides a concise and sometimes amusing synopsis of relative abundance methods with particular reference to insects.

The measurement of relative abundance is enjoying a recent surge in popularity. This stems directly from increased focus on global conservation issues, and the corollary gathering of long-term data on populations. Discussion of relative abundance methods as applied to Lepidoptera is appropriately set in such a conservational context.

Butterfly Counts, and Lepidoptera Conservation

Britain has a long-standing commitment to conserving Lepidoptera and their habitats, and their techniques for studying changes in butterfly and moth populations are accordingly well-developed. Researchers in Britain recognized the "need for a simple reliable method of recording abundance of butterflies in nature reserves and similar places so that changes from year to year can be assessed" (Pollard et al., 1973, p. 79; see also the Scandinavian work by Douwes, 1970, 1976). Out of this need grew the butterfly count—a relative abundance method, broadly defined as a census in which one records the number of individuals seen of different species, according to some predefined spatial and/or temporal rules.

The British have gradually settled on line-transects for butterfly counts, the most prevalent one being that used by the Institute for Terrestrial Ecology (ITE). Briefly, the recorder walks along a pre-determined linear path at a uniform pace, counting butterflies within 5 meters. Counts are made between 1045 and 1545 hours BST; counts are not made when the temperature is below 13°C, only in sunny conditions between 13-17°C, and in any condition other than inclement weather above 17°C. The mean count per transect can be determined on a weekly basis, and these weekly means summed over the entire brood to give an index of abundance. The ITE procedure is an extension of the count technique used in the 1960s by Moore, and is described in depth by Pollard (1977). Thomas (1983) recently established a routine for standardizing counts to allow site-to-site comparisons; let:

L = length of the count transect, in meters
A = size of flight area, in hectares
N = butterfly numbers per 100 meters of transect

$$\text{population index, } P = \frac{100\,N\,A}{L}$$

Ambitious monitoring programs overseen by ITE using the line-transect are underway in Britain; summaries of count results, and their use in

habitat management and ecological research, have been published widely (Pollard, 1977, 1979, 1984).

In North America in 1975, the Xerces Society established its Fourth of July Butterfly Count (4JBC), based on the success of both the British experience and the Christmas bird count of the Audubon Society (Hughes, 1975; the ITE count ultimately also harkens to the Common Bird Census of the British Trust for Ornithology). The 4JBC is a single-day count of butterflies in a circular area, 7.5 miles in diameter from an established central point. The count procedure is fundamentally similar to that described for the ITE line-transect (see Opler and Powell, 1984).

In contrast to the ITE counts, little has yet been done formally with the 4JBC database. Because the 4JBC is only a one day count, the data will obviously be less sensitive to trends than if the censuses were more frequent. But daily/weekly butterfly counts are established in several areas, and studies of trends in relative butterfly abundance in North America are thus becoming available (e.g., Smith, 1984). In general, lepidopteran conservation in the Nearctic is still gathering steam (reviews by Pyle, 1976, and Pyle et al., 1981). Notably, only recently have extensive mark-recapture studies aimed specifically at conserving Nearctic Lepidoptera reached the primary ecological literature (see Arnold, 1983, for lycaenids and *Speyeria* in coastal California; Gall, 1984a, 1984b, for the endemic *Boloria acrocnema* in Colorado).

Reconciling Absolute and Relative Population Estimates

For comparing yearly or site-to-site fluctuations in population size, only relative estimates of abundance are needed. Clearly, though, the ability to calibrate these estimates to reflect the underlying absolute abundances is of great benefit. Relative abundance estimates are usually calibrated by comparison with absolute estimates generated under the same conditions (often on the same day). It is during comparison and especially calibration that the assumptions of relative methods are important. The principal ones are:

1. Either the worker's searching efficiency does not vary in time and/or space, or appropriate allowances can be made
2. Either all individuals are equally sightable, or the sightable fraction remains reasonably constant (analog of "equal catchability")
3. Sighting an individual does not alter the probability of sighting another—or the same individual again, if censuses are repeated frequently (analog of "marking has no effect").

Douwes (1970, 1976), Pollard (1977), and Thomas (1983) have demonstrated that counts of individuals concord highly with population size estimates from MRR models, and calibration can therefore be done

by linear regression (Douwes used the Jolly-Seber model for calibration, Pollard and Thomas several frequency-of-capture models). Thomas (1983) examines the question of calibration in greatest detail, demonstrating that the linearity holds over a rather large range of population sizes. All these authors also nicely document species-specific variation in sightability. For example, Douwes (1976) consistently counted about 30 percent of resident *Heodes virgaureae* and *Clossiana selene* on his transects, whereas Pollard (1977) could count nearly all the *Coenonympha pamphilus*, but less than 25 percent of the *Aphantopus hyperantus*.

These studies on calibrating transect counts are highly encouraging (see also the contributions to line-transect theory made by Gates, 1969, and Sen et al., 1974). Thomas (1983, p. 209) has a cogent argument in that "transect recording [may be] a more accurate way of estimating the numbers of a species that flies infrequently or has large populations, for the recapture rate of marked individuals is then so low that traditional methods yield very poor results." (The question is one of sampling intensity; note that the Fisher-Ford model performs well with scanty data). However, reliance on frequency-of-capture models for calibration is questionable. The problem has two aspects.

First, some field studies (Singer and Wedlake, 1981; Gall, 1984b, and unpublished) on the effects of marking butterflies have shown that, contrary to the investigator's intentions and impressions, even careful marking can perturb subsequent activity. When such mark effects do occur, they are virtually always in the direction of depressing flight activity. Marked butterflies are thus at reduced capture risk, at least temporarily, to both unmarked ones and previously marked ones which have had sufficient time to recover. Because frequency-of-capture models rely upon rapid re-mixing of marks back into the resident population, there will be fewer recaptures than expected. A positive bias in $\hat{N}_i$ results, which in some instances can be as much as double or triple the true population size (see Gall, 1984b, for elaboration). Such bias likely will not greatly confound comparison of *trends* in population size among several sites or years, but it *will* prevent accurate calibration. For example, if mark effects introduce bias linearly over a range of population sizes (as seems reasonable for Lepidoptera), then the slopes of calibration equations will not be affected, but the intercepts will be. This also underscores the point that a marking effect's influence is often invisible unless one makes an explicit test for its presence—which is done surprisingly infrequently.

Second, frequency-of-capture methods have several intrinsic shortcomings. Many generalized truncated distributions can be found which fit the observed recapture classes; however, the unobserved zero-classes implied by these distributions vary widely. Because estimating population size by frequency-of-capture involves sums over all recapture classes, different N_i values can be obtained simply by selecting different truncated distributions. Moreover, these truncated distributions are really

descriptions, not models, and so there is usually no strong rationale for choosing one over another. Cormack (1979, p. 231), addressing Efron and Thisted's (1976) MRR study of Shakespearian text, makes the point succinctly: "different models, wholly consistent with the observed data, give totally different estimates of the population size, even when the observations comprise 31,534 individuals observed in total 884,647 times."

I must again stress that criticism of any abundance model is always context dependent, and the above only pinpoints problems inherent in using frequency-of-capture models to calibrate transect counts, *not* problems inherent in transect counts themselves. The distinction is not trivial—lest the reader take home the wrong message—for transect and other direct counts offer perhaps the simplest, most robust, and least expensive (in the broad sense) methods for indexing butterfly abundance.

DISCUSSION

Historical Impact of Lepidopteran Mark-Recapture Research

Lepidoptera have always occupied prominent positions in the theory and practice of most branches of ecology and evolutionary biology. Mark-recapture is no exception to the rule.

The Fisher-Ford, Jackson, and Schnabel methods are the forebears to all subsequent multiple-marking absolute abundance models. Notably, the Fisher-Ford model was conceived, refined, and tested using Lepidoptera as the study organisms. The initial research included population surveys of the lycaenid, *Polyommatus icarus* (Dowdeswell et al., 1940), the arctiid, *Panaxia dominula* (Fisher and Ford, 1947), and the satyrid, *Maniola jurtina* (Dowdeswell et al., 1949). Indeed, Lepidoptera have greatly influenced the development of most of the more prominent MRR models. As with Fisher-Ford, the Craig (1953) and Manly and Parr (1968) models were conceived with Lepidoptera in mind, the former author using data on *Colias*, the latter data on *Zygaena*. Jolly (1982) uses lepidopteran data for the worked examples of his new models, and the standard texts by Southwood (1978), Begon (1979) and Blower et al. (1981) are illustrated with many such lepidopteran examples.

But the frequent use of butterflies and moths for mark-recapture has had more telling impact on science. The mark-recapture research on *Panaxia dominula* by the British ecological geneticists (using the Fisher-Ford model) is of huge historical significance. These hallmark population studies inaugurated heated transcontinental dialogues on the roles of natural selection and genetic drift in natural populations (e.g., Wright, 1948; [pointed] summary by Ford, 1975). This "selectionist-neutralist" debate has occupied a central role in the development of evolutionary theory ever since. It remains a lively subject today, recast with respect to the significance of electrophoretically detectable enzyme variation, and

reevaluation of neo-Darwinian evolutionary tenets (especially pan-
selectionism; see Lewontin and Gould, 1979).

Three other long term mark-recapture studies of Lepidoptera deserve
mention in this context. First, Kettlewell and his colleagues have used
MRR to examine the operative forces underlying the phenomonon of
industrial melanism, mostly with noctuid and geometrid moths (sum-
mary by Kettlewell, 1973). Second, the 20+ year studies of checkerspot
butterflies by Ehrlich et al. have sparked wide debate on the importance
of gene flow, and the nature of populations as evolutionary units (histori-
cal perspective on *Euphydryas editha* by Ehrlich et al., 1975; Brown and
Ehrlich, 1980, for *E. chalcedona*). Third, the studies by Watt's group on
Nearctic *Colias* butterflies during the last decade successfully link results
from some of the most rigorous mark-recapture work with those from mic-
roevolutionary genetics. Their biochemical (Watt, 1983; Watt el al.,
1983) and populational (Watt et al., 1977, 1979) articles detailing the
action of natural selection on structural gene polymorphisms set the
current standard for the discipline.

Thoughts for the Future

What, then, remains to be done? Regarding mark-recapture theory in
general, there are still four major needs, among others: (1) models free
from the assumption of independence of successive samples, an assump-
tion breached by marking effects in their broadest sense; (2) models to
measure local movement patterns, and an interface from these to MRR
models; (3) means for dealing with very large populations; and (4) com-
prehensive models with greater parsimony (Jolly, 1982, has taken the
major step in this direction).

Topic two, measuring local movement, touches upon a problem central
to all biological field work—defining the limits of populations. Mark-
recapture is the technique for measuring movement patterns, and I
expect that studies of Lepidoptera will contribute significantly to advan-
ces in this area, as they have in the development of MRR models (already,
butterflies have figured in recent innovative work on local movement:
e.g., Jones et al., 1980; Kareiva, 1982). Moreover, such mark-recapture
studies will prove of great value to conservationists, for local movement
patterns define (1) the physical boundaries of a population, (2) its inter-
connectedness with other populations, and hence (3) effective neigh-
borhood sizes. Mark-recapture also provides data on (4) effective
population sizes, and in combination these four factors are relevant to
understanding extinction and colonization probabilities, the general sub-
ject of which is reviewed by Soule and Wilcox (1980). Similarly, the first
two factors are useful in the design and maintenance of preserves. For
example, the movements of individuals pinpoint the location of dispersal
corridors, and hence offer insight into how to partition parcels slated for

development i.e., don't build across the major dispersal corridors (opportunity for re-colonization would otherwise be drastically reduced).

As aptly noted by Murphy (1984), in a tart review of Arnold's (1983) mark-recapture surveys of endangered California butterflies, our Palearctic counterparts have amassed embarassingly large leads in the practice and politics of invertebrate conservation. This is quite true, and it is novel mark-recapture research that will go far toward establishing parity. Thus, although some of Murphy's caveats deserve to be heeded, I cannot recommend in the least his assertion (p. 268) that: "in essence the results of mark-recapture studies, no matter how rigorous, and natural history investigations, no matter how detailed, by themselves tell us virtually nothing at all about the extinction vulnerability in butterflies."

Age structure in adult Lepidoptera is a subject well deserving of final mention. The usual index of butterfly age is physical wing wear—most often scale loss, but sometimes cuticular damage. While correlations between age and indices of one or both aspects of wear have been independently discovered and reported many times, only recently has age structure been integrated quantitatively into lepidopteran MRR studies. Watt et al. (1977, 1979) and Tabashnik (1980) were the first to do so, focusing principally on age-specific patterns in residence. Extension of this research into catchability and movement has been productive, with perhaps the most intriguing finding being that sex-age-specific movement may be a widespread pattern, highlighted by emigration of old females (see Gall, 1984a, 1984b, 1984c).

A sobering conclusion from these MRR studies is that failure to consider age structure often entirely masks crucial biological patterns. The extent to which age, when not treated, confounds the results of most published studies of lepidopteran biology is as yet unclear, but I judge it to be a potentially explosive problem (Gall, 1984c, for discussion). Age-specific movement also bears directly on the needed refinements in MRR theory outlined above, and so I feel that a quantitative framework for dealing with lepidopteran age structure is likely to be among the more important future contributions to the field of mark-recapture. Because lepidopteran age can be indexed so simply, I am also optimistic for rapid progress in this area.

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Lowland Riparian Butterflies of the Great Basin and Associated Areas

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Abstract. Many species of butterflies are characteristic of or restricted to
riparian habitats in the valleys of the Great Basin region. These belong to
three elements based on distribution: northern, southern and widespread.
Southern species richness decreases upstream from the Colorado River.
Northern species richness decreases downstream and towards the central
Great Basin from two distinct, but related, centers: the Humboldt River
drainage and the western Nevada drainages. Distribution patterns resemble
those demonstrated for birds.

The Great Basin of western United States is a large area of mainly inter-
nal drainage between the Rocky Mountains and the Sierra Nevada. It
includes western Utah, most of Nevada, and portions of eastern California,
southern Oregon and southern Idaho. The overriding context of the Great
Basin is aridity. Most biological interest has centered in the many more
mesic mountain ranges where diversity tends to be greatest. For each
mountain range, however, there are associated valley systems which have
received little study. Several of these valleys are relatively well watered
by rivers or intermittent streams, some are fed by springs and still others
are dry. The Colorado River and its tributaries drain portions of the
southern Great Basin area and tributaries of the Snake River drain the
extreme northern portion. The remainder of the region has no ex-
ternal drainage.

Biogeographic affinities and distributions of Great Basin fish have been
analyzed by Smith (1978). Johnson (1978) discussed lowland riparian dis-
tributions of birds. Until recently, the distributions of butterflies in the
Great Basin were largely unknown, especially in the valleys. I have col-
lected considerable data from such situations over the last several years.
These are now adequate to allow an analysis of the riparian butterfly dis-
tribution of the Great Basin, especially Nevada, and immediately adja-
cent areas.

Drainages and Habitats

The name "Great Basin" is a misnomer. It is not one large basin but is a
physiographic province composed of numerous smaller drainage areas

many of which are presently unconnected. Nevada, alone, contains 14 hydrographic regions and basins. These each contain a number of hydrographic areas for a total of 232 in Nevada (Anonymous, 1971). The regions can be grouped into three categories: (1) mostly linear basins with major rivers (Snake, Humboldt, Truckee, Carson, Walker and Colorado), (2) basins with no major stream flow (Black Rock Desert, Great Salt Lake, Escalante Desert and Death Valley) and (3) regions with groups of mostly closed and often dry valleys (Northwest, Western, West Central and Central). Further discussion and the water dynamics of these areas were presented by Anonymous (1971).

The intermountain valleys of Nevada are vegetated by one of several shrub communities. In southern Nevada, these are dominated by creosote bush *(Larrea tridentata)*. In more saline areas in the south, and especially further north in western Nevada, shadscale *(Atriplex confertifolia)* is predominant. The third major valley community which occurs over most of the remainder of Nevada is an extensive and monotonous sagebrush *(Artemisia tridentata)* community.

Riparian communities of various types occur along water courses in many of the major valleys, in some of the smaller valleys and near springs and seeps. These may be extremely diverse biologically and cover substantial habitat area or be depauparate, quite small and isolated. Occurring along many streams are stands of cottonwood *(Populus fremontii)* and willow *(Salix* spp.). Occasional marshes and wet meadows occur. Further from the main channels, especially on alkaline soils, are associations dominated by iodinebush *(Allenrolfea occidentalis)* and saltgrass *(Distichlis spicata)*. The latter is often the only riparian vegetation in poorly watered valleys. There is an additional kind of riparian association in southern Nevada consisting principally of an aborescent growth of phreatophytic mesquites *(Prosopis* spp.) and acacia *(Acacia greggii)*.

Methods

I collected most of these data during the last ten years at 65 sites in Nevada and southwestern Utah (Fig. 1). The Nevada localities include 12 of the 14 delineated hydrographic regions of the state. Locations were visited on several occasions at selected times of the year to obtain as complete a seasonal representation of the butterfly fauna as possible. Species lists were developed from these collections in addition to records from others and the literature (especially Emmel and Emmel, 1973; Ferris and Brown, 1981).

A rather diverse assortment of taxa were included as riparian components of the butterfly fauna (Tables 1, 2). All are principally distributed in and many are restricted to association with riparian vegetation at lowland sites in Nevada. A number similarly occur in wet
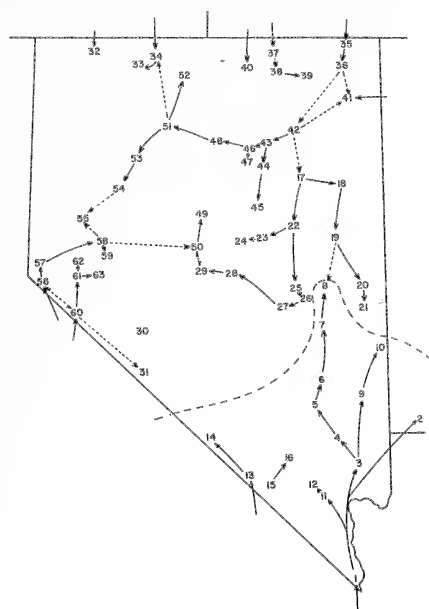
Fig. 1. Sample sites for riparian butterflies in the Great Basin and associated areas. Numbers refer to localities keyed in Tables 1 and 2. Solid arrows indicate closest phyletic relationships (generally in direction of decreasing faunal diversity); dashed arrows indicate relationships between hydrographic regions. Dashed line indicates approximate boundary between northern and southern riparian butterfly faunas.

places in montane situations. Included are species commonly associated with the activities, usually agricultural, of man (e.g., *Colias eurytheme, C. philodice, Pieris rapae)*. Also included is *Pieris protodice* which occurs over a broad range of habitats in early spring and occasionally in fall, reaching its greatest abundance at wetter areas through the summer. Most taxa, however, are closely associated with riparian vegetation among which they find their larval foodplant. Excluded are principally montane taxa which occasionally are found and sometimes breed in the riparian valleys (e.g., *Hesperia comma, Nymphalis milberti, Limenitis weidemeyerii)*, various ubiquitous species which are not particularly associated with wet areas (e.g., *Pyrgus communis)* and wandering, sporadic and otherwise unclassified taxa.

Two species warrant special mention. *Plebejus melissa* is represented in southern Nevada by a distinctive phenotype restricted to lowland sites in the Colorado River drainage. Further north, nominate *melissa* occurs in riparian situations but also in several other habitats and is not included as a riparian species. *Polygonia satyrus* is also a riparian species and

occurs at some of the northern Nevada sites. Its presently known distribution is spotty and it is excluded from the tabulations.

Species Composition

The butterfly fauna of the Great Basin valleys is composed of a number of species which are narrowly and usually disjunctly distributed wherever suitable habitat occurs. Away from the immediate riparian vegetation, whether saltgrass flats or marshes, riparian associated butterflies are usually absent. A total of 62 taxa belonging to 46 species are considered typical of or restricted to these riparian habitats (Table 1, 2). These belong to three distributional elements: (1) a southern group (25 taxa) with largely desert affinities, (2) a northern group (30 taxa) with diverse affinities and (3) a widespread group (7 taxa) most with a wide distribution throughout North America. The occurrence and distribution of these groups and of the individual taxa themselves correspond to drainage basins (Table 1, 2). The southern taxa, with the exception of nonpermanent populations or strays, occur exclusively in the Colorado River and Death Valley drainages and in the southernmost Central Region of Nevada. Northern taxa occur primarily in the remainder of the state. There is very little overlap; seven of the northern taxa occur in various combinations with southern taxa at six northern sites of the Colorado River drainage.

The southern species are most diverse along the Colorado River from southern Nevada southward (Table 1). There is little dilution along the lower portions of two of its tributaries (Virgin and Moapa rivers, Fig. 2).
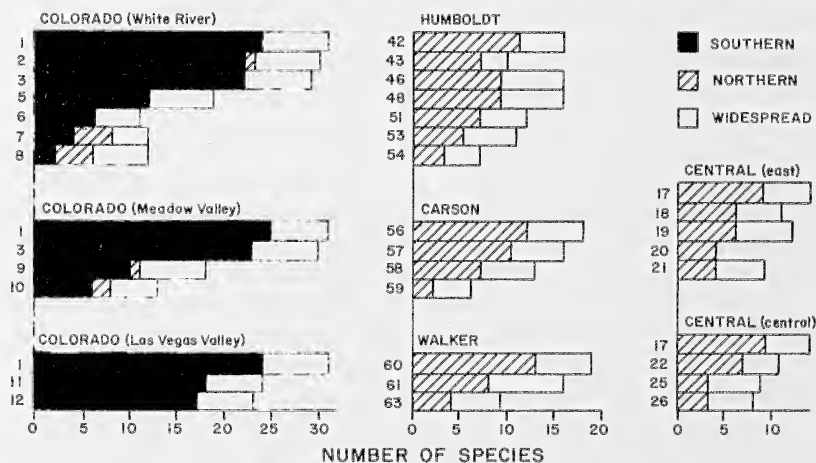
Fig. 2.   Taxa group composition of riparian butterfly faunas in the Great Basin and associated areas. Numbers on vertical axis refer to sample sites as keyed in Tables 1 and 2.

The drier Las Vegas Valley (to Corn Creek) still has a fair diversity of species. North of these areas and corresponding to a general increasing isolation of riparian habitat, a marked reduction in the number of species is found. Relative abundance seems to decline in many species also. The most northern points (Lund, Sunnyside, Hiko, Ursine) have six or fewer southern species. The decline in species richness may reflect distance from source populations, isolation and possibly the severity of winters. Suitable larval foodplants are present north of these southern species' distributions. For example, willow (*Salix*), the host of *Limenitis archippus*, occurs at most sample stations but the butterfly occurs only along the Colorado River and its immediate tributaries. Mesquite (*Prosopis*), the host of *Apodemia palmerii* and *Ministrymon leda*, similarly occurs in Meadow Valley but not the butterflies. Other examples exist.

The two sample sites each from the Death Valley Basin and the southern Central Region are inhabited by a depauparate assemblage of Colorado River Basin species and both show similar upstream impoverishment. Only one species (*Pseudocopaeodes eunus*) unknown in the Colorado drainage occurs in the Death Valley Basin.

Brephidium exilis has a distribution similar to the southern taxa but regularly wanders northward in summer, often occurring (and breeding) at the northern border of the state. How far north *exilis* is permanently established has not been determined (and it is not included in the tabulations). A number of the other southern taxa irregularly wander northward and are occasionally found, sometimes breeding, at northern stations. These include *Nathalis, Precis, Danaus, Leptotes* and both species of *Hemiargus*. Their permanent residency appears to be within the limits of the southern group distribution (but perhaps not as far as indicated in Table 1), and thus all northern Nevada records are excluded from the tabulations.

Northern drainages in Nevada collectively have more taxa than the southern drainages (Table 1, 2) but have fewer species (17 vs. 25). Individual drainages, however, have considerably fewer taxa than the Colorado River Basin (Table 2). The number of species decreases more gradually from the periphery inward than in the south (Fig. 2). Nine of the 11 northern species ocurring along the Humboldt River at Elko are still present as far downstream as Dunphy and Battle Mountain and seven occur at Winnemucca. The Reese River hydrographically is a tributary of the Humboldt River but has none of the latter's endemics and instead has taxa from both the Carson/Walker drainages and the Central Region. This may be partially a result of the discontinuity of the downstream portion of the Reese River where there is very little riparian vegetation.

In the Central Region, seven and six of the nine northern species at Ruby Valley occur as far as Newark and Steptoe valleys, respectively.

Outlying points in this region have noticeably impoverished local faunas. No northern species are found at Mina and only *Polites sabuleti* is found at Monitor Valley. *Colias philodice* and *P. sabuleti* are at Fish Lake Valley (the phenotype of the latter is closer to that in the Carson and Walker drainages than to those at other Central Region sites). Seven additional sites (Spring, Lake, Antelope, Kobeh and Railroad valleys, Duckwater and Currant) have two to four northern group species (all have *Polites sabuleti* and five have *Hesperia uncas*).

Generalizations about the Snake River Basin localities in Nevada are more difficult. These are upstream sites of drainages extending north into Idaho from which no specific site data are available. A composite list generated from Ferris and Brown (1981) indicates a maximum of 10-12 northern species present in the main Snake River drainage. The faunas of the Nevada sites (Table 2) thus are only a somewhat impoverished representation of the Snake River fauna. The Nevada points basically are all similar in species composition and related to those of the Central Region and the Humboldt River Basin.

Three similar river systems exist in western Nevada. The relatively wet (compared with other Great Basin mountains) east slope of the Sierra Nevada and nearby mountains support extensive areas of adjacent valley riparian vegetation with an associated riparian butterfly fauna in the Truckee, Carson and Walker river basins. Both the number of species involved and the gradual impoverishment downstream in the Carson and Walker basins (Fig. 2) is similar to that occurring in eastern Nevada.

All the drainages and regions in northern Nevada are rather similar. The relatively small number of upstream species and the gradual decrease downstream (except possibly the Snake drainage, see above) are a common theme which distinguishes them from the southern drainages. Of the 17 northern species, seven occur in all five of the major northern drainages and regions for which there is sufficient data (Carson, Walker, Snake, Central, Humboldt) and four others occur in four of the five (Table 2). Three species are restricted to the Carson and/or Walker basins and two to the Snake and/or Humboldt basins. *Hesperia uncas* occurs in the Central Region and in the Humboldt and Walker river basins.

One further feature alluded to above distinguishes the southern drainages from the internal drainage basins of the north. In the Colorado River Basin (and apparently the Death Valley Basin and the southern Central Region) the riparian faunas are rich downstream and become depauparate upstream. The converse is true in the Humboldt, Carson and Walker basins. In these, the greatest species richness is in the upper portions of the major valleys. This reflects a basic physiogonomic difference between the two. The southern valleys drain relatively arid mountains and most eventually empty into a major river, the Colorado, with external drainage. The northern valleys drain well watered mountains

and terminate in internal, alkali sinks. The unifying feature is faunal impoverishment towards the central Great Basin and richness peripherally (also well illustrated by the Central Region data).

One other area must be discussed along with the possible influence of man's activities. The Truckee River Basin of western Nevada has been connected by canal (completed in 1905) to the Carson River Basin through Fernley in the West Central Region. Considerable riparian vegetation occurs along the canal banks and undoubtedly provides a dispersal corridor across otherwise uninhabitable desert. The fauna of the area (e.g., Fernley) is most closely related to that of the Carson and Walker drainages (Table 2). The general area (Wadsworth to Fallon of the Truckee and Carson basins) is the only area where *Limenitis archippus* of eastern Nevada flies with *L. lorquini* of western Nevada.

Phenotypic Differentation

Refinement of the pattern described above at the species level to a lower taxonomic level (subspecies, etc.) reveals a more complex situation. In northern Nevada, *Pseudocopaeodes eunus* occurs in the Walker, Truckee and Carson river basins only as a downstream species. Most are of a bright phenotype near *P. e. wrightii* but the Eagle Valley population in the Carson River basin is distinct and approaches nominate *P. eunus* in phenotype. Whether the Truckee basin *P. eunus* (dispersal from the Walker basin) and the occurrence of *L. archippus* in the Carson and Truckee drainages (dispersal from the Humboldt basin) is recent (post-canal) or not is unknown. *P. e. wrightii* also occurs in two isolated colonies in the Reese River and Big Smoky valleys.

The *Polites sabuleti* of the Truckee, Carson, Walker and most of the Humboldt river basins and of the Black Rock Desert Region are phenotypially similar to nominate *P. sabuleti*. Another similar population occurs in Fish Lake Valley in the western part of the Central Region. The eastern portion of the Central Region is inhabited by a very dark *P. sabuleti* phenotype which is undescribed. In central Nevada, including the southernmost sites of the Central Region (Newark, Railroad, Big Smoky, Montir, etc. valleys) and Humboldt River Basin (Reese River), there are very pallid populations of *P. sabuleti* which again are undescribed. In the Big Smoky Valley and Reese River area, a particularly pallid and unique *Cercyonis oetus (pallescens)* occurs.

The Walker, Carson, Truckee and most of the Humboldt drainage are inhabited by a large and pale *Satyrium sylvinus* seemingly near *desertorum*. In the Snake River Basin and Central Region, *S. sylvinus* is represented by *putnami*. This is a widespread Rocky Mountain taxon in the eastern Great Basin. At the extreme northern (Paradise Valley) and southeastern (Alpha) sample sites of the Humboldt River basin, the

sylvinus are assignable to the nominate subspecies and *putnami*, respectively. The phenotype of *Limenitis archippus* near nominate *archippus* occurs in the Snake drainage while *L. a. lahontani* is nearly restricted to the Humboldt drainage (see above). *Coenonympha ampelos ampelos* occurs in all northern drainages except in the Humboldt Valley (but the population at Reese River is also phenotypically this subspecies) and in Ruby Valley. The subspecies *elko* is restricted to the Humboldt and Ruby valleys. Similarly, the *Cercyonis pegala* of eastern and western Nevada differ subspecifically. The Snake and Humboldt river basins and the Central Region are inhabited by several similar undescribed populations which have minor but identifiable differences in some valleys (e.g., between Steptoe Valley and Newark Valley). The Carson Valley *pegala* is much different (something allied to but not *gabbii*) and another *pegala* (resembling the phenotype in eastern Nevada) is found in the upper Walker River drainage.

The Northwestern Region which extends into northeastern California and south-central Oregon is represented by a single sample site in Nevada. The butterflies of this site are of complex affinities (Table 2) and the area has an endemic *Cercyonis pegala* subspecies (*stephensi*). Another *Cercyonis pegala*, a *gabbii*-like insect (but different from that of Carson Valley), occurs in the Black Rock Desert Region. *Lycaena rubidus* and *Satyrium sylvinus* here are of the nominate phenotypes.

The fauna of certain northern points of the Colorado River drainage, as mentioned above, contain northern group species. *Satyrium sylvinus putnami* occurs at three of these. The *Polites sabuleti* at Sunnyside is similar to the phenetically dark populations occurring from Ruby Valley to Steptoe Valley in northeastern Nevada. Similarly, the *Cercyonis pegala* of the Lund area is more like that in Steptoe Valley than the one in Newark Valley. *Hesperia uncas* of the White River Valley (Lund, Sunnyside) are of a pale, low elevation phenotype similar to *lasus*. The population of *Speyeria nokomis* at Ursine is an isolate (as are all populations of this species). All of these represent the southernmost occurrences of the taxa in the Great Basin of Nevada.

All areas of both northern and southern drainages have between three and seven widespread species. One, *Ochlodes yuma*, is widespread but occurs only in isolated pockets with its foodplant (Scott et. al., 1977) and is apparently absent from the Snake and Carson river basins. The absence of the widespread *Vanessa atalanta* appears to be due to the scattered distribution of its host, *Urtica*. *Pieris protodice* and *Colias eurytheme*, on the other hand, occur at every sample station. The remaining species occur at an intermediate number of sites (Table 1, 2).

The southern species uncommonly occur away from the lowland riparian habitat. A few (e.g., *Leptotes, Hemiargus, Precis, Danaus*) are

encountered in montane situations but only as summer residents or wanderers. These are the same taxa which establish apparently non-permanent colonies north of the southern drainages. Their centers of abundance are in the lowlands. Many of the northern taxa, in contrast, have distributions which extend into the wetter mountain canyons. Only *Pseudocopaeodes, Hesperia, Polites* (except in a very few situations), *Papilio, Strymon sylvinus* ssp., *Phyciodes pratensis* ssp., *Limenitis archippus, Coenonympha ampelos elko* and *Cercyonis pegala* seem restricted largely to the valleys. Similarly, all of the widespread riparian species, except *Ochlodes*, also have partly montane distributions.

Discussion

The riparian distribution of Great Basin butterflies is strikingly similar to the distribution of riparian birds (Johnson, 1978). There are northern and southern bird taxa groups with replacement coincident with that found for butterflies at the approximate northern limits of the Death Valley and Colorado River basins (Fig. 1). Impoverishment away from major drainages and into the central Great Basin is common to both birds and butterflies. Similarly, the general decrease in species richness inward from the periphery of the Great Basin is found in montane bird faunas (Johnson, 1975, 1978; Brown, 1978), mammals (Brown, 1978), plants (Harper et al., 1978) and butterflies (unpubl. data). In fish, there is an increasing impoverishment from the periphery to the interior of the Great Basin (Smith, 1978). Endemism is considerably higher in fish, as is expected of a taxonomic group with low dispersal capacity, than in butterflies and, especially, birds. However, fish tend to be more broadly distributed in the north, unlike butterflies.

The partial two way gradient with distribution centers and some phenotypic differentiation in eastern and western Nevada, respectively, suggests that the butterflies of the eastern and western drainages of the northern portion of the Great Basin in Nevada have had somewhat separate evolutionary histories. Dispersal and/or differentiation is probably post-Pleistocene in most or all instances with isolation of populations increasing as the huge Pleistocene lakes dried. Differences between the Humboldt and the Carson and Walker drainages are indicative of this (Table 2). Dispersal differences involves species occurring in one drainage group but not the other (*Speyeria cybele, Limenitis*) and subspecific differentiation (*Phyciodes, Coenonympha, Cercyonis*) between the two source areas. Yet a common history as part of the Lahontan drainage is indicated by the occurrence in both areas of relatively undifferentiated *Polites* and *Satyrium*. Furthermore, *Hesperia uncas, Polites sabuleti, Cercyonis pegala*, and *Cercyonis oetus* show a degree of infrasubspecific differentiation in some areas (especially in the Central Region) of the Great Basin.

Preliminary evidence indicates that valley systems can act as island centers of evolution similar to (and possibly stronger than judging from the comparative degree of phenetic differentiation) montane islands. Additional collecting and comparisons are needed, however, to further refine degrees of affinity between isolated valley populations. *Speyeria nokomis* in Ruby Valley, for instance, show definite phenetic similarity with the more eastern nominate *nokomis*, an attribute not shared with other populations of the species considered here (see also Ferris and Fisher, 1971).

The distributions of the taxa listed in Tables 1 and 2 can be viewed on a yet broader biogeographic scale than in the previous section: (1) taxa widely distributed in western United States or beyond, (2) taxa regionally distributed across several drainage basins or hydrographic regions but not restricted to the Great Basin and (3) endemic taxa. The biogeographic affinities of the southern group is principally with the North American deserts to the south. Most species are also regional, occurring in more than one drainage basin. *Pholisora gracielae* and possibly the *Plebejus melissa* ssp. appear endemic to the Colorado River Basin and *Pseudocopaeodes eunus alinea* is endemic to the Death Valley Basin. The northern group of taxa has complex affinities. Some (*Polites sabuleti sabuleti, Pieris occidentalis, Colias philodice, Lycaena rubidus, Plebejus saepiolus*) are widespread through much of the northwestern United States. In eastern Nevada, *Satyrium sylvinus putnami* and *Phyiodes pratensis camillus* with Rocky Mountain affinities are definitely regional in their Great Basin range. They occur in the Central Region, Snake River Basin, southern sites of the Humboldt River Basin and at northern points in the Colorado River Basin. *Papilio oregonius* and *Limenitis archippus archippus* have a northern distribution and reach their southern limits in the northern Great Basin. In western Nevada, *Satyrium sylvinus sylvinus, Speyeria cybele leto, Phyciodes pratensis pratensis, Limenitis lorquini* and *Coenonympha ampelos ampelos* have their centers of distribution in the Sierra Nevada and westward. The remainder of the northern taxa are largely Great Basin endemics at the subspecies level. Some are narrowly restricted to individual drainages (e.g., an undescribed *Phyciodes pratensis* in the Humboldt River Valley) and several others occur in two or more hydrographic regions.

The theory of island biogeography has been widely applied to the biota of the montane islands of the Great Basin (Johnson, 1975, 1978; Brown, 1971, 1978; Harper et al., 1978) and, as can be seen here, certainly also apply to the disjunct patches of riparian habitat in the valleys. Present distributions of these riparian habitat restricted butterflies give some indication of their dispersal patterns and capacity, of barrier and distance effects resulting in depauparate faunas and of rates of differentiation. There is evidence also of modern local extinction of one species,

Ochlodes yuma, due both to natural causes and to human activities. The larval foodplant of this skipper, *Phragmites communis*, has a wide, but patchy distribution in the Great Basin. The plant and consequently the insect have been eliminated by man from at least two Nevada sites (Tule Springs, Clark County and Lida, Esmeralda County). Near Mina (Mineral County) exists a still healthy colony of *Phragmites,* but the once present *O. yuma* has disappeared. Other extensive and apparently suitable stands (e.g., at Carson Lake) harbor no *O. yuma* possibly the result of local extinction. The lack of a fossil record or even historical records, however, preclude inferences on the role of extinction on present distribution patterns. Some butterfly species absences clearly are due to absence of proper foodplants. Whether other absences are the result of some combination of butterfly dispersal incapabilities, chance or extinction is a matter of conjecture.

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Table 1. Riparian butterflies of the Colorado River and associated drainages in southern Nevada.[1,2]

	COLORADO RIVER BASIN												DEATH VALLEY REGION BASIN		CENTRAL REGION (south)	
	1 Colorado River	2 Virgin River	3 Overton/Moapa	4 Coyote Springs	5 Pahranagat Valley	6 Hiko	7 Sunnyside	8 Lund	9 Meadow Valley	10 Ursine	11 Las Vegas	12 Corn Creek	13 Ash Meadows	14 Beatty	15 Pahrump	16 Indian Springs
SOUTHERN GROUP																
Erynnis funeralis	X	X	X	–	–	–	–	–	–	–	X	–	–	X	–	–
Pholisora libya libya	X	X	X	X	X	–	X	–	X	–	X	X	X	X	–	X
Pholisora gracielae	X	X	X	–	–	–	–	–	–	–	–	–	–	–	–	–
Copaeodes aurantiaca	X	X	X	–	X	–	–	–	–	–	X	X	–	–	–	–
Hylephila phyleus muertovalle	X	X	X	–	X	–	–	–	X	–	X	X	X	X	X	X
Pseudocopaeodes eunus alinea	–	–	–	–	–	–	–	–	–	–	–	–	X	X	–	–
Polites sabuleti chusca	X	X	X	–	X	–	–	–	–	X	X	X	X	X	X	X
Atalopedes campestris campestris	X	X	X	–	X	X	–	–	–	–	X	X	X	X	X	–
Lerodea eufala	X	X	X	–	X	–	–	–	–	–	X	X	X	X	X	–
Eurema nicippe	X	X	X	X	–	–	–	–	–	–	X	X	X	X	–	–
Nathalis iole	X	X	X	X	–	–	–	–	X	–	X	X	X	–	X	–
Atlides halesus estesi	X	X	X	X	–	–	–	–	X	–	X	X	X	–	X	X
Ministrymon leda	X	X	X	X	–	–	–	–	–	–	X	–	X	–	X	–
Leptotes marina	X	X	X	X	X	X	–	–	X	X	X	X	X	–	X	X
Hemiargus ceraunus gyas	X	X	X	X	X	X	–	–	X	X	X	X	X	X	X	X
Hemiargus isola alce	X	X	X	X	X	X	X	–	X	X	X	X	X	X	–	X
Plebejus melissa ssp./3	X	X	X	–	X	X	X	X	X	X	–	–	–	–	–	–
Calephelis nemesis californica/4	X	X	X	–	–	–	–	–	–	–	–	–	–	–	–	–
Calephelis wrighti	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Apodemia palmerii palmerii/5	X	X	X	X	–	–	–	–	–	–	X	X	X	–	X	X
Chlosyne lacinia crocale	X	X	X	–	–	–	–	–	–	–	X	X	–	–	–	–
Phyciodes tharos distincta	X	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–
Precis coenia	X	X	X	–	X	X	X	X	X	X	X	X	X	X	–	–
Limenitis archippus obsoleta	X	X	X	–	–	–	–	–	–	–	–	–	–	–	–	–
Danaus gilippus strigosus	X	X	X	X	X	–	–	–	X	X	X	X	X	X	X	X
NORTHERN GROUP																
Hesperia uncas lasus	–	–	–	–	–	–	X	X	–	–	–	–	–	–	–	–
Polites sabuleti ssp./6	–	–	–	–	–	–	X	–	–	–	–	–	–	–	–	–
Colias philodice	–	–	–	–	–	–	X	X	–	–	–	–	–	X	–	–
Satyrium sylvinus putnami	–	X	–	–	–	–	–	–	X	X	–	–	–	–	–	–
Speyeria nokomis apacheana	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–	–
Phyciodes pratensis camillus	–	–	–	–	–	–	X	X	–	–	–	–	–	–	–	–
Cercyonis pegala ssp./6	–	–	–	–	–	–	–	X	–	–	–	–	–	–	–	–
WIDESPREAD GROUP																
Ochlodes yuma	X	X	X	–	X	X	–	X	X	–	X	X	X	X	–	–
Pieris protodice	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Pieris rapae	X	X	X	X	X	X	X	X	X	–	X	X	X	X	X	–
Colias eurytheme	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Lycaena helloides	X	X	X	–	X	X	X	X	X	X	–	–	–	–	X	X
Nymphalis antiopa	X	X	X	–	X	–	–	X	X	X	X	X	–	X	X	–
Vanessa atalanta rubria	X	X	X	–	X	–	–	–	X	X	X	X	X	–	–	–

Table 2. Riparian butterflies of the northern Nevada drainages.[1,2]

Column groupings (regions / drainages):

- CENTRAL REGION (north)
- NORTHWEST REGION
- BLACK ROCK DESERT
- SNAKE RIVER BASIN
- GREAT SALT LAKE BASIN
- HUMBOLDT RIVER BASIN
- WEST CENTRAL REGION
- CARSON RIVER BASIN
- WALKER RIVER BASIN
- TRUCKEE RIVER BASIN

Localities (columns):

17 Ruby Valley
18 Currie
19 Steptoe Valley
20 Spring Valley
21 Lake Valley
22 Newark Valley
23 Antelope Valley
24 Kobeh Valley
25 Buckwater
26 Currant
27 Railroad Valley
28 Monitor Valley
29 Big Smoky Valley
30 Mina
31 Fish Lake Valley
32 Dufurrena
33 Kings River Valley
34 Quinn River Valley
35 Jackpot
36 Contact
37 Mountain City
38 Wildhorse
39 Charleston
40 Independence Valley
41 Thousand Springs
42 Elko
43 Carlin
44 Pine Valley
45 Alpha
46 Dunphy
47 Beowawe
48 Battle Mountain
49 Central Reese
50 Reese River
51 Winnemucca
52 Paradise Valley
53 Rye Patch
54 Lovelock
55 Fernley
56 Carson Valley
57 Eagle Valley
58 Stillwater
59 Carson Lake
60 Sweetwater
61 Mason Valley
62 Wabuska
63 Schurz
64 Washoe Lake
65 Wadsworth

NORTHERN GROUP

Pseudocopaeodes eunus wrighti
Pseudocopaeodes eunus eunus
Hesperia uncas lasus
Polites sabuleti sabuleti
Polites sabuleti ssp./3
Polites sabuleti ssp./4
Papilio oregonius
Pieris occidentalis
Colias philodice
Lycaena rubidus sirius/5
Satyrium sylvinus sylvinus
Satyrium sylvinus ssp./6
Satyrium sylvinus putnami
Plebejus saepiolus saepiolus
Speyeria cybele leto
Speyeria nokomis apacheana/7
Phyciodes pratensis pratensis
Phyciodes pratensis camillus
Phyciodes pratensis ssp./8
Limenitis archippus archippus
Limenitis archippus lahontani
Limenitis lorquini
Coenonympha ochracea mono
Coenonympha ampelos ampelos
Coenonympha ampelos elko
Cercyonis pegala stephensi/9
Cercyonis pegala ssp./10
Cercyonis pegala ssp./11
Cercyonis pegala ssp./12
Cercyonis pegala gabbii

WIDESPREAD GROUP

Ochlodes yuma
Pieris protodice
Pieris rapae
Colias eurytheme
Lycaena helloides
Nymphalis antiopa
Vanessa atalanta rubria

Footnotes for Table 1:

[1]Numbers preceding locations correspond to those in Fig. 1

[2]More precise locations are as follows (all Nevada unless indicated):
1. lower valley from about Blythe, Riverside Co., CA to Davis Dam, Clark Co. (some data from Emmel and Emmel, 1973)
2. vicinity of St. George, Washington Co., UT (some data from Ferris and Brown, 1981)
3. Muddy River Valley, Overton to Moapa, Clark Co.
4. spring along U.S. 93, Lincoln Co.
5. valley south of Alamo, Lincoln Co.
6. northern Pahranagat Valley, vicinity of Hiko, Lincoln Co.
7. White River Valley, Wildlife Management Area, Nye Co.
8. White River Valley, county line to Preston, White Pine Co.
9. Meadow Valley Wash, Elgin to Caliente, Lincoln Co.
10. Spring Valley, north of Ursine, Lincoln Co.
11. Las Vegas Valley, vicinity of Las Vegas, Clark Co.
12. spring area, Desert National Wildlife Range, Clark Co.
13. spring area, Nye Co.
14. Amargosa Valley, Beatty to Springdale, Nye Co.
15. Pahrump Valley, vicinity of Pahrump, Nye Co.
16. Indian Springs and Cactus Springs, Clark Co.

[3]a distinct valley phenotype

[4]the apparently distinct *dammersi* has been recorded at Blythe and Overton

[5]*marginalis* is a synonym

[6]allied to the Steptoe Valley population (see Table 2)

Footnotes for Table 2:

[1]numbers preceding locations correspond to those in Fig. 1

[2]more precise locations are as follows (all Nevada):
17. National Wildlife Refuge area, Elko Co.
18. swales north and south of Currie, Elko Co.
19. vicinity of Warm Springs, White Pine Co.
20. vicinity of Shoshone, White Pine Co.
21. vicinity of Geyser Ranch, Lincoln Co.
22. 20-30 miles north of U.S. 50, White Pine Co.
23. along U.S. 50, west of Eureka, Eureka Co.
24. along U.S. 50, 13 mi. E Lander Co. line, Eureka Co.
25. wet areas near Duckwater, Nye Co.
26. Currant to 10 miles west, Nye Co.
27. vicinity of Lockes, Nye Co.
28. vicinity of Potts, Nye Co.
29. Carvers to Lander Co. line, Nye Co.
30. springs in vicinity of Sodaville, Mineral Co.
31. north of Dyer, Esmeralda Co.
32. Sheldon Antelope Range, Humboldt Co.
33. vicinity of Kings River, Humboldt Co.
34. Orovada to McDermitt, Humboldt Co.

35. south of Jackpot, Elko Co.
36. vicinity of Contact, Elko Co.
37. just south of Mountain City, Elko Co.
38. Wildhorse Creek Campground area, Elko Co.
39. vicinity of Charleston Reservoir, Elko Co.
40. south of Jack Creek, Elko Co.
41. Thousand Springs Creek, Elko Co.
42. vicinity of Elko, Elko Co.
43. just south of Carlin, Elko Co.
44. Pine Creek Valley, 20-30 miles south of Elko Co. line, Eureka Co.
45. Alpha Ranch area, Eureka Co.
46. just west of Dunphy, Eureka Co.
47. Beowawe to geyser area, Eureka/Lander cos.
48. along Humboldt River, north of Battle Mountain, Lander Co.
49. Reese River Valley, Nev. 305, 18-30 mi. N U.S. 50, Lander Co.
50. Reese River Valley in vicinity of U.S. 50, Lander Co.
51. just west of Winnemucca, Humboldt Co.
52. vicinity of Paradise Valley, Humboldt Co.
53. Rye Patch Dam to Mill City, Pershing Co.
54. north of Lovelock, Pershing Co.
55. canal just south of Fernley, Lyon Co.
56. south of Genoa, Douglas Co.
57. east of Carson City, Carson City
58. Fallon to Stillwater National Wildlife Refuge, Churchill Co.
59. U.S. 95, 11-13 mi. S Fallon, Churchill Co.
60. wet areas adjacent to East Walker River near CA line, Lyon Co.
61. Mason Valley near Yerington, Lyon Co.
62. spring area just north of Wabuska, Lyon Co.
63. vicinity of Schurz, Mineral Co.
64. vicinity of Washoe Lake, Washoe Co.
65. Truckee River in Wadsworth area, Washoe/Storey cos.

[3] very dark phenotype
[4] series of pallid populations, more than one taxon may be involved
[5] population at Dufurrena is closer to nominate *rubidus* than to *sirius*
[6] large pale phenotype, often tailless
[7] Ruby Valley population shows influence of nominate *nokomis*
[8] very pallid phenotype
[9] *blanca* is a synonym
[10] *gabbii* may not be the correct name, the phenotype was previously referred to *ariane*
[11] more than one taxon may be involved
[12] very different from Carson Valley population, shows some similarity to populations in northeastern Nevada

The Pupa of *Lotisma trigonana* and Some Characteristics of the Copromorphidae (Lepidoptera)

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Abstract. The pupa of *Lotisma trigonana* (Walsingham), one of two Nearctic copromorphid genera, is described. Comparisons with the pupae of two other Copromorphidae indicate that positions of head and thoracic features and movable abdominal segments 5-10 are characteristic of the family. Rearing observations indicate that larval feeding mode, hostplant family, cocoon construction, and overwintering stadium are variable among the Copromorphidae.

Introduction

Even though Mosher (1916) recognized its value in determining taxonomic affinities over a half century ago, the pupa rivals the egg as the most neglected stadium in descriptions of Lepidoptera. There are few or no descriptions of the pupae of many genera and several smaller families. Consequently, characterization of the pupae of many groups is difficult or impossible on the basis of published information alone. Such is the case with the Copromorphidae, a small tropical family, with only two Nearctic genera.

Prior to the transfer of *Lotisma trigonana* (Walsingham) to Copromorphidae (Heppner, 1978), that family was not thought to be represented in the Nearctic region. Subsequently, a second Nearctic genus, *Ellabella* Busck, was transferred to Copromorphidae (De Benedictis, 1984). In that paper, the pupa of *Ellabella bayensis* Heppner is described and illustrated, but apparently few or no other copromorphid pupae have been described in detail. Fletcher (1933, pl. xv), for example, illustrated the pupa of an Indian species, *Copromorpha myrmecias* Meyrick, but it lacks detail, and there is little descriptive information in the text.

The pupa of *L. trigonana* is described here and compared to that of *E. bayensis*. Because the Copromorphidae are poorly known, I also describe some observations from collecting and rearing both species.

Material Examined

I obtained larvae of *L. trigonana* by collecting whole inflorescences of madrone, *Arbutus menziesii* Pursch (Ericaceae), on a ridge two miles

north of Alpine Lake, Marin County, California, on April 16, 1983. The larvae are well concealed in the inflorescences, terminal panicles of dense racemes of small, creamy-white flowers. Except for a black head capsule and cervical shield, a small reddish dorsal anal patch and, occasionally, two faint subdorsal lines, flower-feeding *L. trigonana* larvae are almost exactly the same color as madrone flowers. They usually feed within the urn-shaped flowers, so frass-fouled silk which ties together several flowers provides the best visual evidence of the concealed larvae.

There were four or five species of Lepidoptera larvae in the inflorescences. Those matching the description of *L. trigonana* larvae by MacKay (1972) were isolated from the other larvae and reared on cut flowers in plastic bags. Other species included one or two species of geometrids which I was unsuccessful in rearing and two eucosmine Tortricidae, *Epinotia emarginana* (Walsingham) and *E. terracoctana* (Walsingham).

Four larvae and two pupae of *L. trigonana* were preserved by boiling in water then transferring to 95% ethanol. Twenty adult moths emerged from the remainder of the lot between May 6 and June 1, 1983, two to four weeks after pupation.

The frail pupal shell turned transparent in alcohol which made examination of morphological features difficult, so drawings were made from a live pupa with the aid of a camera lucida attached to a Wild binocular dissecting scope. Later, the pharate adult became visible which facilitated the identification of the morphological features of the pupa.

Description of the Pupa (Figs. 1 & 2)

Length: 5.3-5.5 mm; somewhat pliant, but frail; appearing white except eyes pink in young pupae, darkening to black later. **Head:** Frons somewhat flattened apically; antennae extending to wing tips at anterior margin of A9, not meeting along ventral meson; eyes prominent; pilifers present as small lobes mesad of eyes; maxillary palpi present as triangular lobes posterio-laterad of eyes; haustellum extending from eyes and pilifers nearly to wing tips; labial palpi along ventral meson from clypeus to mid-metathorax. **Thorax:** Prothorax narrow, collar-like; mesothoracic wings extending to anterior margin of A9, not meeting along ventral meson and free from A5-9; metathoracic wings almost entirely concealed; forelegs extending to A3, nearly meeting at ventral meson; mesolegs laterad of forelegs, extending to middle of A6; tarsi of hindlegs visible between wing tips caudad of haustellum. **Abdomen:** A1-4 slightly longer than caudal segments; A5, 6, and 7, and 8-10, as a unit, movable; A5, 6, and 7 encircled with mid-segmental ridge; spiracles inconspicuous, on protruding lobes on A2-4; cremaster of seven setae, six in a caudal row, one more anteriad on ventral meson.

Remarks: The pupal shell is somewhat pliant, but delicate and easily damaged by handling. The mid-segmental ridge on segments A5-7 probably strengthens them. There are some very fine paired setae in lateral rows on A5-7 and on the dorsum of A7 and 8. These setae usually broke when the pupa was extracted from its cocoon and were easily confused
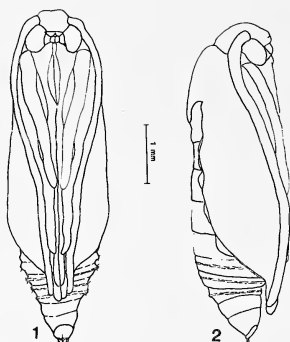
Figs. 1 & 2. Pupa of *Lotisma trigonana* (Walsingham). **1.** Ventral aspect. **2.** Lateral aspect. (Vertical line = 1.0 mm).

with remnants of silk, so exact numbers and locations of setae could not be determined. Some may have been overlooked. These setae clearly were not strong enough to anchor the pupa to the cocoon. The abdomen lacks true spines and spurs. The pupal shell does not protrude from the cocoon when the adult emerges. The movable abdominal segments telescope into the anterior segments upon adult emergence.

Discussion

Although the larval description by MacKay (1972) was adequate for identification, the larvae I collected differed in that the pinnacula were poorly differentiated and less conspicuous than those in her illustration. The semicircular submental lobes, which she suggested are characteristic of the family, were very small and could easily be overlooked.

In addition to madrone, known larval hostplants of *L. trigonana* larvae are several other members of the heather family (Ericaceae). These include fruit and flowers of manzanitas (*Arctostaphylos* spp.), salal (*Gautheria shallon* Pursh), and evergreen huckleberry (*Vaccinium ovatum* Pursh) (Llewellyn-Jones, 1937; Powell, unpubl. rearing notes).

Larvae in my collection which matured after the cut madrone flowers wilted were provided with manzanita berries into which they bored or fed upon externally. Unlike the larvae which matured while feeding upon flowers, fruit-feeding larvae were almost entirely reddish in color rather than creamy-white with reddish markings. The reddish color was very similar to that of the berries.

Feeding mode and hostplant family is variable among the Copromorphidae. *Ellabella bayensis* feeds externally upon the flowers and, from rolled shelters, on foliage of coastal barberry, *Mahonia pinnata* (Lagasca) Fedde (Berberidaceae) (De Benedictis, 1984). *Copromorpha myrmecias* bores into twigs of figs, *Ficus* spp. (Moraceae) (Fletcher, 1933).

The cocoon of *E. bayensis* is a rolled leaf lightly lined with silk (De Benedictis, 1984) while that of *L. trigonana* is a fluffy mass of loose, cream-white to buff silk spun in crevices or between overlapping leaves. Fletcher (1933) states that *C. myrmecias* pupates within the larval burrow but does not mention a silken cocoon.

The pupae of *L. trigonana* and *E. bayensis* both exhibit head and thoracic features at approximately the same locations. Both species have the same movable abdominal segments and bear the spiracles of A2 and 3 on triangular lobes. Such lobes are visible in the illustration of the pupa of *C. myrmecias* as well (Fletcher, 1933, pl. xv). The spiracles of A4 on *L. trigonana* are also borne on such lobes.

Fletcher's (1933) illustration of the pupa of *C. myrmecias* depicts more dorsal setae than are present on either *L. trigonana* or *E. bayensis*. Such differences suggest that positions of pupal setae vary at the generic or specific level.

Fletcher (1933) does not mention whether the pupal shell of *C. myrmecias* protrudes from the larval burrow, but non-protrusion, the absence of true spines and spurs, and the concentration of the setae of the cremaster at the tip of the terminal abdominal segment probably are characteristic of the entire superfamily Copromorphoidea.

The apparently more heavily sclerotized pupal shell and tighter cocoon of *E. bayensis* may be adaptations to its overwintering as a pupa. Emergence data and flight records of adult *L. trigonana* suggest that it overwinters as an adult.

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A Tropical Caterpillar that Mimics Faeces, Leaves and a Snake (Lepidoptera: Oxytenidae: *Oxytenis naemia*)

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Abstract. The tropical moth *Oxytenis naemia* shows four different mimicry strategies during its life, including characteristics such as false eyes and snake-like display. The uniqueness of the combination of these mimetic strategies reflects a high selection pressure, which appears to be typical for tropical ecosystems.

Introduction

It is a widespread phenomenon that some animals are inconspicuous because they resemble naturally occurring objects like bark, a leaf, a twig, or inedible objects. This phenomenon is termed mimicry (Edmunds, 1981) and serves to help the animal escape detection by predators or prey. When insects at first resemble objects of a limited size (e.g. ants) subsequent instars of the species must mimic different objects. Many praying mantids have first instars which resemble ants, whereas later instars and the adults mimic leaves, grass blades or bark (Edmunds, 1976). In holometabolous insects, which pass through morphologically different life stages, each stage can mimic a different model. Caterpillars and sphingid, geometrid and bombycid moths are especially well known for changing their mimicry strategy during their lives (Cott, 1940). The present case deals with *Oxytenis naemia* Druce, 1906, (Oxytenidae), a moth of tropical Panama.

Materials and Methods

The moth *Oxytenis naemia* is a representative of the strictly neotropical family Oxytenidae (superfamily Bombycoidea) which contains some 36 species. *Oxytenis* moths are mainly brown and yellow (Watson and Whalley, 1975) and most of them resemble dry leaves when resting. *Oxytenis naemia* is known from tropical Costa Rica and Panama to Peru and Paraguay. It is a medium-sized moth which lays its eggs exclusively on the leaves of a few species of Rubiaceae shrubs, mainly *Isertia haenkeana*.

The study was carried out in the vicinity of Gamboa, Panama, in a tropical lowland forest. Approximately 50 oxytenid larvae were collected

from several locations near Gamboa between August and October 1983 and were individually raised on leaves of *Insertia haenkeana* (Rubiaceae) in the laboratory (25-32°C, 75% r.h., LD 12:12; = standard Gamboa conditions, Nentwig, 1985).

Results

Oxytenis larvae of instars one-three are black and have many small spines and a short, forked tail. Their resting position is in the form of a "J", the anterior part of the body being bent towards the first abdominal segments and touching them. In this position the head is concealed and the whole animal resembles bird dung. In all instars of *O. naemia* the third thoracic segment is enlarged and forms small wing-like structures. These structures camouflage the overall shape of the caterpillar and emphasize the general impression of a bird's dropping (Fig. 1a). The fourth instar differs in colour from the foregoing stages. The larvae are rather brown, often quite light, sometimes yellowish, and appear somewhat oily, so resembling the faeces of some other animal, probably a large bird. These faeces-like instars last altogether approx. 10-14 days.

In the fifth and final instar (duration 4-9 days) the caterpillar changes its mimicry strategy again and resembles a fallen, rolled-up leaf. This effect is produced by a triangular pattern on the front part of the body which gives the impression of the open end of a rolled leaf. The main colour is now a velvet brown; some parts of the caterpillar are light to dark brown, but the whole animal may instead be velvet green, red-brown or pink (Fig. 1b). Thus some of the fifth instar caterpillar population mimic freshly fallen green leaves and others resemble dried or drying leaves. There are additionally triangular patterns on the sides of the abdomen. In most individuals they are divided into single spots or else they are completely lacking (Fig. 2). These spots are sometimes darker than the caterpillar thus resembling holes in the leaf. In other larvae they are silver-white (especially if the larva is green) and may resemble a fungus infection, or small faeces dots.

When these leaf-mimicking caterpillars are disturbed most do not form a "J" (which would not suit the strategy of mimicking a rolled-up leaf), but instead show a curious display which has been described independently by several observers as "snake-like". Two spots located dorsally on the enlarged thoracic section resemble a pair of half-closed eyes. By pumping haemolymph into the thorax, a fold of the thoracic skin is expanded and the eye spots enlarge. These large false eyes now consist of a black pupil with a yellow iris and even show a touch of white in the upper corner. This gives the impression of light reflections as in a real vertebrate eye (Fig. 1c). Sometimes the caterpillar rears up and waves the anterior third of the body. In this posture a pair of bright yellow spots on the underside of the enlarged thoracic part becomes exposed. These are
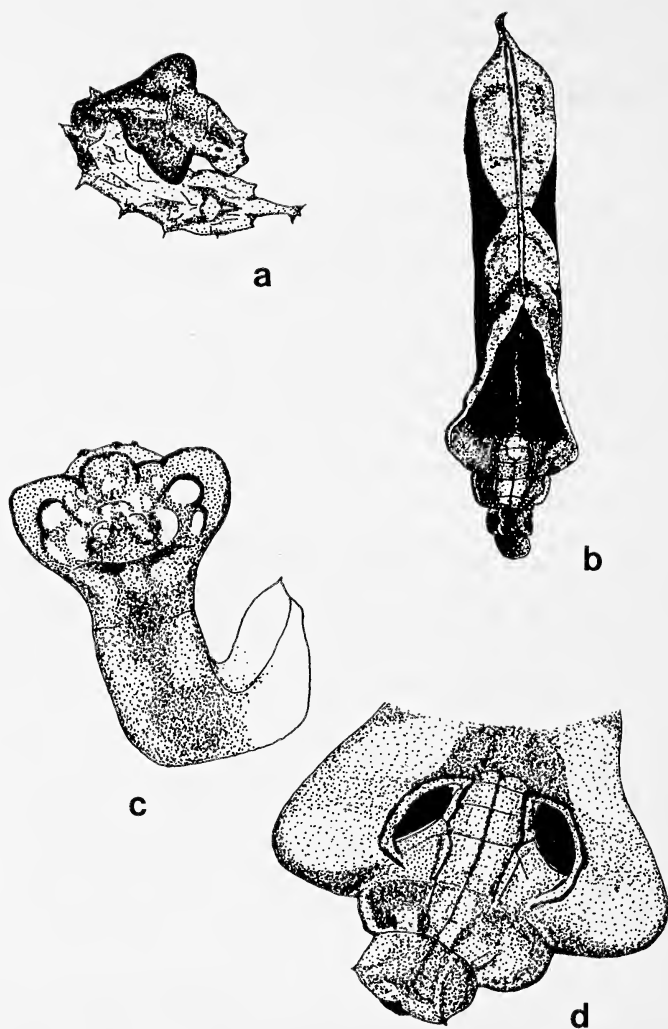
Fig. 1. The mimicry strategy of *Oxytenis naemia* caterpillars: (redrawn
schematically from slides).
   a.   The third larval instar mimics dark faeces (dorsal view).
   b.   The third larval instar mimics a rolled-up leaf (dorsal view).
   c.   When the caterpillar is disturbed, large false eyes appear on the
        thorax (fifth instar, anterior view).
   d.   When more disturbed, the caterpillar rears up, waves the anterior
        third of the body, and shows additional false eyes on the underside
        (fifth instar, dorsal view).
   Caterpillar length ca. 20 mm (a) and 40-50 mm (b-d).
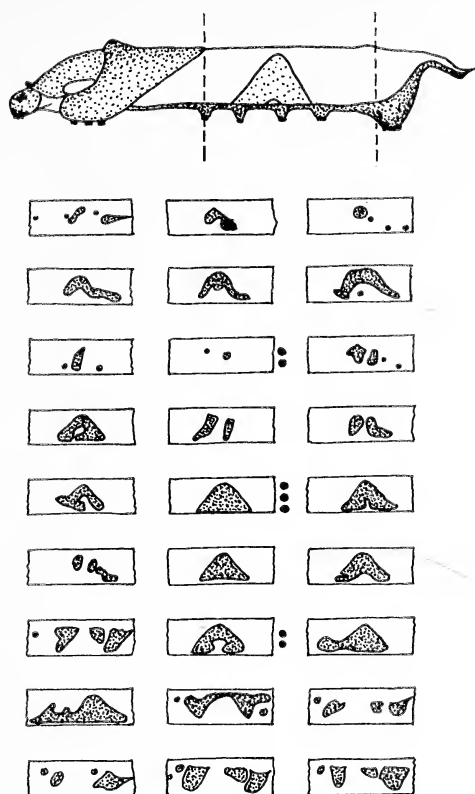
Fig. 2. Fifth instar of *O. naemia* (lateral view, schematically), showing the high variation of the lateral patterns (area between the dotted lines). Dots mark patterns which occurred twice or three times; three larvae had no patterns.

certainly imitations of eyes as well (Fig. 1d). The opening of the false eyes and the turning behaviour is so impressive that Hingston (1932) who saw it in the Guiana forest described it as a cobra display.

Finally, after the prepupal stage (one day) and pupal stage (9-14 days) the moth ecloses. In colour pattern and posture of the wings the resting moth resembles a dry, fallen leaf. This mimicry includes the normal movement of a falling leaf. When disturbed, only a small number of *O. naemia* specimens move their wings like a normal moth or butterfly. Most fall to the ground, holding their wings in the resting position (Aiello, pers. comm.), and 'disappear' in the litter layer like a real dead leaf, completely escaping one's view.

Discussion

Oxytenis naemia possesses four different mimicry strategies. First they resemble 1) small, dark faeces; next 2) large, lighter faeces; then 3) rolled leaf and flat leaf. In addition, 4) morphological and behavioural adaptations enable the animal to show false eyes and a snake-like appearance. The adults resemble dead leaves and appear to fall to the ground when disturbed. All these capabilities are known from other caterpillar species, but it is unique to find them all realized in one species. Curio (1965) reports snake-mimicry in the neotropical sphingid *Pholus labruscae*. Moss (1920) studied the Brazilian sphingid *Leucorampha ornatus*, which in addition to a snake-like display enlarges the thorax and shows its underside, where two dark, symmetrical eye-spots appear. Such behaviour and mimicry is usually explained as a response to strong predator pressure. The same is indicated by the irregular distribution of the caterpillars over their one food plant. Over large areas *O. naemia* larvae are absent, then they occur on one shrub in a relatively high density (three to five larvae). The larvae in these groups are of the same age, which reflects the special oviposition behaviour of the female moth. The changes in shape, colour and general appearance of the larvae may make it difficult for a predator to obtain a search image for larvae of this species. Moreover, this is accentuated by a variable behaviour: some larvae form a "J", some do not, and some show snake display. The colour pattern is highly variable in the last instar, as well as in the adult moths. In the genus revision, Jordan (1924) has noted that the typical three black dots on the male forewing are sometimes absent but he was not aware of the full range of variation in colouring. In males, wings vary from a bright brown to the common dark, greyish brown. Females also vary from a dark, male-like colour to a more typical light brown.

The population losses due to parasites were high among the sample larvae (these had been collected in the field and raised in the laboratory). An unidentified microorganism (possibly a virus) was present in 21% of the individuals and had the effect of changing the internal consistency of the pupae to a muddy liquid within a few days. Another further 21% of the original larval population (= 33% of the surviving pupae) were parasitized by a tachinid fly (1-10 flies per pupae, average = 4.0). On one occasion these flies were observed attacking a leaf-mimicking instar of *O. naemia* in the field. The caterpillar defended itself successfully by the snake-like display indicating that the interpretation of this behaviour exclusively as a cobra display (Hingston, 1932) is perhaps too restrictive. It is difficult to imagine that a 50-mm-caterpillar mimics a snake, especially a cobra on a leaf, as defence against a parasitic fly. The main parasitism by the tachinids occurs in the early faeces-mimicking instars which do not show the snake-like behaviour. This leads to the conclusion that the latter display is not directed against parasites, but probably

towards potential vertebrate predators. Arboreal venomous vine snakes occurred frequently in the study area, some of which are small—at least when young. Curio (pers. comm.) points out that the head of some poisonous snakes are very small, and, in many cases, the full body length of the snake cannot be seen. Thus, the 50-mm-caterpillar would represent only the visible part of a much longer snake. Generalized eye-spot markings as a defence mechanism are wide-spread in the animal kingdom (Wickler, 1968) and their anti-predator effect has been demonstrated (Blest, 1957). Consequently, it may be difficult to discriminate between a specialised snake display and a more generalized anti-predator behaviour, where snake-like movements are only one feature among other frightening characteristics.

The multiple mimicry strategy of *O. naemia* supports earlier assumptions (e.g., Dobzhansky, 1950; Robinson, 1978) that in tropical ecosystems predator pressure, parasitism, and other interspecific actions are the main cause of mortality. Here they are held to be the major selective force, whereas temperate zones climatic conditions are thought to be more important. In the tropics mimicry phenomena are extremely common, and interactions between species can be very complex. Further research will certainly reveal additional equally bizarre examples of protective colouration and behaviour.

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The Identification of Two Species of *Junonia* Hübner (Lepidoptera: Nymphalidae): *J. evarete* and *J. genoveva* in Jamaica

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Abstract. The validity of the two species *Junonia evarete* and *Junonia genoveva* originally described by Cramer from Surinam is re-established and recognized in Jamaica. The relevant literature of this group is reviewed and the synonymy of these species is discussed. Morphological, behavioral and chromosomal differences between the adults of the two species are discussed and notes on the life histories and immature stages are included.

Introduction

Since Hübner (1819) described the genera *Precis* and *Junonia*, much controversy has occurred as to whether the type species that were later designated for the two genera were congeneric. Whether the use of *Precis* or *Junonia* should be adopted is not within the scope of this paper, but we have agreed with Comstock's (1944) argument here to retain the name *Junonia* for the Jamaican buckeyes.

The first major revision of the group was published by Forbes (1928) who used the name *lavinia* (Cramer, 1775) for all Central American, American, Caribbean and South American races of *Junonia*. Comstock (1942) subsequently pointed out the invalidity of the name *lavinia* and proposed the next available name *evarete* (Cramer, 1779). As the types of *lavinia* and *evarete* both were described from Surinam, they were thought to be conspecific, and Comstock (1944) used the new specific name *evarete* and recognized three Puerto Rican subspecies, *J. e. coenia* (Hübner), *J. e. zonalis* (C. and R. Felder) and *J. e. genoveva* (Cramer).

Bates (1935) had previously treated *Junonia* (= *Precis*) *coenia* and *J.* (= *Precis*) *zonalis* as distinct species in Cuba. Munroe (1949) retained subspecific rank for *J. e. coenia* and *J. e. zonalis* and stated, "in Cuba, the equivalent of a species difference exists between the two forms *coenia* and *zonalis* which are almost identical in genitalia". Munroe (1951)

separated *J. coenia* as a distinct species from three forms of *J. evarete*, namely *zonalis, michaelesi,* and *evarete.* He designated these three *evarete* forms as "wet and dry" phenotypes comparable to phenological variants seen in related Old World forms. He, however, reported that on some West Indian islands, both forms occur together in the same season, and on other islands, one or other form appears to be absent. Torre y Callejas (1971, 1974) retained the specific rank of *J. coenia* but recognized several forms of *J. evarete zonalis* in Cuba.

In Jamaica, *J. coenia* has never been recorded. Avinoff and Shoumatoff (1946) listed two species from Jamaica, *J. zonalis* (Felder) and *J. genoveva* (Cramer). They further recorded that *J. zonalis* was abundant in open fields but that they did not collect *J. genoveva.* Brown and Heineman (1972) followed Munroe (1951) in regarding *zonalis* and *genoveva* as wet and dry forms of a single species *Precis evarete* Cramer (= *Junonia evarete* Cramer).

We regard Comstock's (1944) *Junonia evarete zonalis* and *J. e. genoveva* as distinct species in Jamaica. The establishment of specific names for these two species was made by reference to the original drawings of Cramer (1779, Plate 203, C & D) for *J. evarete* and Cramer (1780, Plate 290, E & F) for *J. genoveva.* The relevant parts of these plates are reproduced here as Figure 1. Although both of these species were originally described from Surinam and the original types were destroyed, the plates and the descriptions enabled us to identify the two Jamaican species. Thus we propose to discontinue using the name *zonalis* (Felder & Felder) and use *J. evarete* (Figs. 2 and 3) and *J. genoveva* (Figs. 4 and 5) for Jamaican specimens.

Cramer's (1779) drawings of *J. evarete* show no distinct eyespots on the underside of the hindwings and a greatly restricted fascia on the upperside of the forewings. This form is similar to the uncommon species in Jamaica which was until now referred to as the *genoveva* form of *J. evarete.* Cramer's (1780) description and drawings of *J. genoveva* show specimens with well developed eyespots on the undersides of the hindwings and a wide pale fascia on the upperside of the forewings. These types resemble the common species in Jamaica hitherto known as *J. evarete zonalis.* The significance of this is that the buckeye *Junonia zonalis* or *Junonia evarete zonalis* hitherto referred to by many authors as occurring commonly in many West Indian islands, in fact should be referred to as *J. genoveva.* Conversely, the less abundant insect, formerly referred to as *J. genoveva* or *J. e. genoveva,* is in fact correctly identifiable as *J. evarete.*

The morphology and ecology of the adults and the biology of their immature stages have been studied by the senior author between 1962 and 1979, primarily from material collected at Holland Bay, Palisadoes and Green Bay in Jamaica where there are large, permanent sympatric

populations of *J. evarete* and *J. genoveva*. A total of 214 preserved specimens comprising 55 males and 38 females of *J. evarete* and 70 males and 55 females of *J. genoveva* were used for compilation of data during this study. These specimens were from the senior author's collection and from the collection at the Institute of Jamaica. Twenty-four males and 21 females of *J. coenia* from Florida, from the Rutkowski collection were also studied for comparative purposes.

Synonymy

Original identifications and Jamaican, Caymanian, Cuban and Puerto Rican descriptions only.

Junonia evarete (Cramer)

Papilio lavinia Cramer, 1775, Vol. 1, p. 32, pl. 21, C, D.
Papilio evarete Cramer, 1779, Vol. 3, p. 18, pl. 203, C, D.
Junonia lavinia lavinia f. *genoveva* Forbes, 1928, 305-321.
Precis lavinia f. *genoveva* Carpenter & Lewis, 1943, p. 384.
Junonia evarete genoveva Comstock, 1944, p. 455, pl. 6, fig. 13; Riley, 1975, p. 74.
Junonia genoveva Avinoff and Shoumatoff, 1946, p. 279; Wolcott, 1936, p. 399, Wolcott, 1941, p. 122.

Junonia genoveva (Cramer)

Papilio genoveva Cramer, 1780, Vol. 4, pl. 290, E, F.
Junonia zonalis C. & R. Felder, 1867, p. 399; Avinoff and Shoumatoff, 1946, p. 279.
Junonia genoveva (Larval description only) Swainson, 1901, p. 79.
Junonia lavinia f. *zonalis* Forbes, 1928, p. 307.
Precis zonalis Bates, 1935, p. 77; Wolcott, 1936, p. 399.
Junonia lavinia Wolcott, 1936, p. 398.
Precis lavinia f. *zonalis* Carpenter & Lewis, 1943, p. 385.
Junonia evarete zonalis Comstock, 1944, p. 454; Munroe, 1951, p. 9; Torre y Callejas, 1954; 1971, p. 24; 1974, p. 11; Riley 1975, p. 74.
Junonia evarete michaelesi Munroe, 1951, p. 10.
Junonia evarete evarete Munroe, 1951, p. 13.
Precis evarete zonalis Brown & Heineman, 1972, p. 179.
Junonia evarete Riley, 1975, p. 74.

Diagnostic Features Separating the two Species

ADULT CHARACTERS

The adults may be distinguished by reference to Table 1 and Figures 2-5. The color and extent of the sub-apical fascia on the forewings, the dis-

tribution of orange color sub-marginally on the hindwings dorsally and the ground color and maculations on the hindwings ventrally are the chief distinguishing features. There are also minor differences in wing size, some wing markings and in the coloration of the antennae.

Examination of male genitalia, testes and chromosomes provides further evidence for separation of *J. evarete* and *J. genoveva*. Carpenter and Lewis (1943) studied variation in dentition of the inner process of the terminations of the male valves in a sample of 30 *Junonia* in and around the Caribbean, including nine males from Jamaica, and noted that there was much variation in the number of spines, even on opposite valves of the same specimen.

We conducted a more detailed study of the same portion of the genitalia. We counted all the terminal spines present on both valves (at 200 x magnification) from a sample of 15 males each of *J. evarete* and *J. genoveva* and compared mean numbers of spines for each species statistically. The mean valve spine number for *J. evarete* is 17.4; (n = 15, range 12 to 21) and for *J. genoveva* the mean valve spine number is 27.6; (n = 15, range 18 to 35). *J. genoveva* has significantly more spines than *J. evarete* (t = 7.29, 28 d.f., P = 0.001). The 95% confidence limits for the difference in mean spine number between the two species is 10.2 ± 2.98. Because there is a small overlap of spine numbers between the two species, this character will only serve to separate populations, not individuals.

The paired testes of *J. evarete* are dark brown and noticeably larger than the pink testes of *J. genoveva*. This difference was consistent in 13 specimens of *J. evarete* (26 testes) and 16 specimens of *J. genoveva* (32) testes.

Chromosome preparations of the specimens made by T. C. Emmel show that both *J. evarete* and *J. genoveva* have the same chromosome number (n = 31). However, *J. evarete* has "three notably smaller chromosomes" whilst *J. genoveva* possesses "four definitely smaller chromosomes". Emmel (pers. comm.) concludes, "on the basis of consistent karyotypes in your two sets of material sent to date. . .I would say you have two species involved rather than the one according to Brown and Heineman (1972)". The specimens featured in Figures 2-5 have all been deposited with the Allyn Museum of Entomology, Sarasota, Florida.

IMMATURE STAGE CHARACTERS

The eggs of both species are sub-globose, flattened at base and micropyle, with twelve vertical ribs which terminate around the micropyle. They are of similar size, varying between 0.65-0.68 mm in diameter at the base and between 0.58-0.61 mm in height. They can only be identified by their presence on their respective specific foodplants.

Although the larvae of *J. evarete* are always larger than those of *J. genoveva* at a similar stage of development, there is one consistent
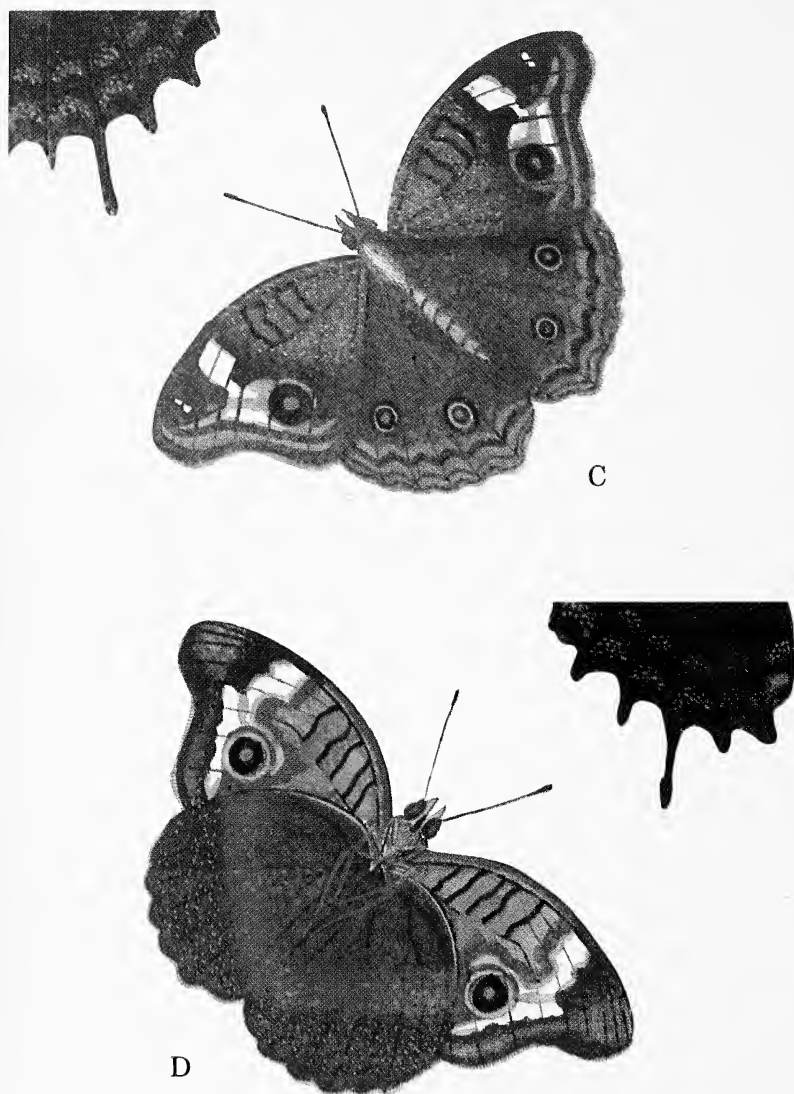
Fig. 1.   Cramer's types.
          Junonia evarete 1779, Plate 203. C. Dorsal, D. Ventral
          Junonia genoveva 1780, Plate 290. E. Dorsal, F. Ventral

E
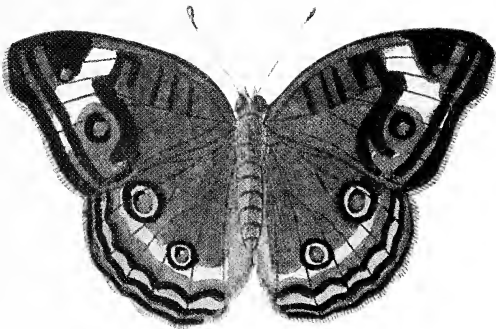
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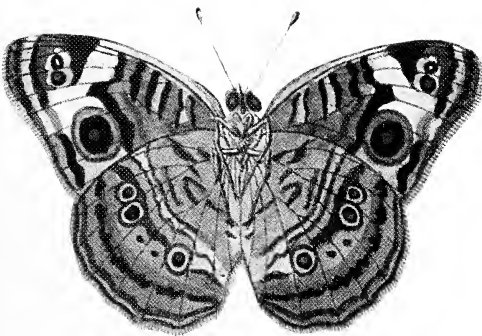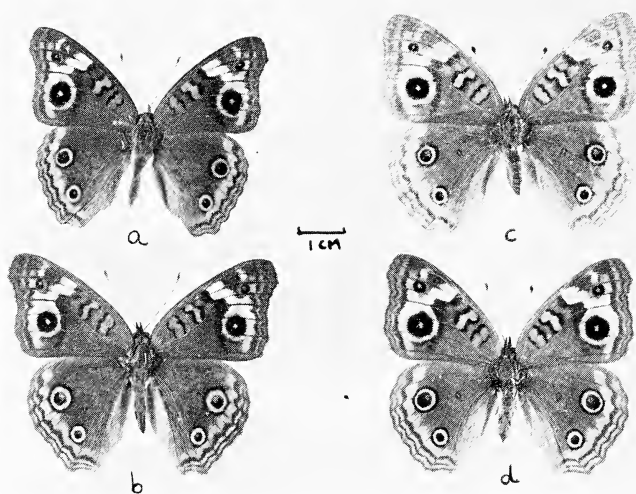
Fig. 2.   Jamaican *Junonia evarete*, dorsal aspect.   **a.** Male. T. Turner, Holland Bay, St. Thomas. January 14, 1968, Jamaica. W.I.   **b.** Male. T. Turner, Holland Bay, St. Thomas, July 29, 1966, Jamaica W.I.   **c.** female. Bred T. Turner, Holland Bay, St. Thomas, January 10, 1969, Jamaica W. I.   **d.** Female. T. Turner, Holland Bay, St. Thomas, July 29, 1966, Jamaica W.I.
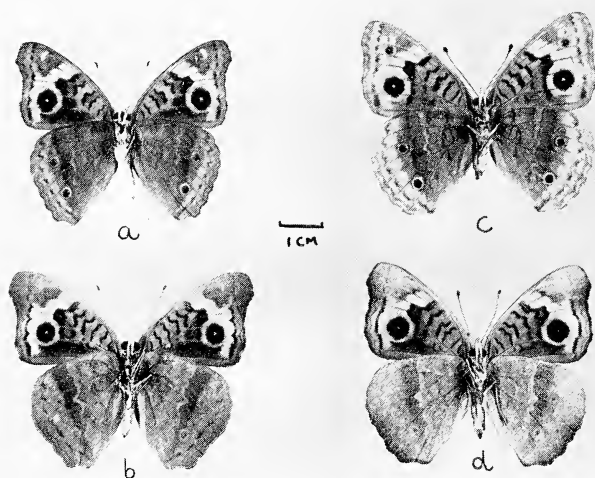
Fig. 3.   Jamaican *Junonia evarete* ventral aspect. Legend as for Fig. 2.
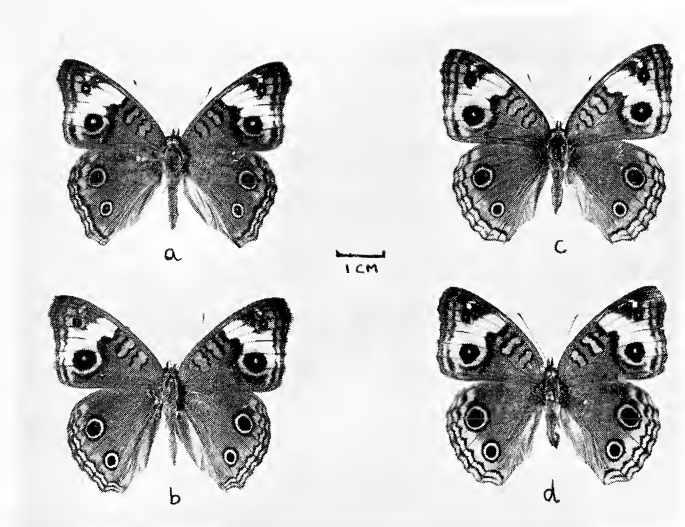
Fig. 4.   Jamaican *Junonia genoveva*, dorsal aspect.   **a.** Male. Bred T. Turner,
Mona, St. Andrew, January 1, 1968, Jamaica W.I.   **b.** Male. Bred T. Tur-
ner, Holland Bay, St. Thomas, August 7, 1966, Jamaica W.I.   **c.** Female.
T. Turner, Roselle, St. Thomas, January 14, 1968, Jamaica W.
I.   **d.** Female. T. Turner, Tower Hill, St. Andrew, July 31, 1966,
Jamaica W.I.
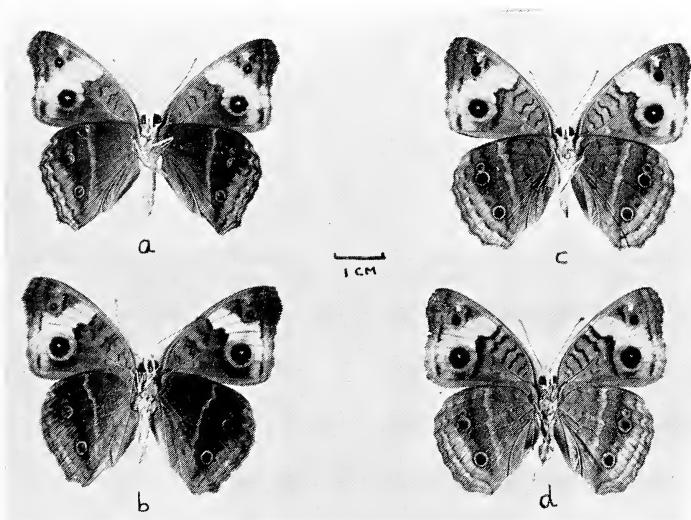
Fig. 5.   Jamaican *Junonia genoveva* ventral aspect. Legend as for Fig. 4.

Table 1.   Features distinguishing the adults of *Junonia evarete* from those of *Junonia genoveva* in Jamaica W.I.

EVARETE	**GENOVEVA**
a) Fascia of forewings	
Dorsally restricted especially between veins M2 and M3; distinctly tawny. Vein M3 black and conspicuous across fascia. Ventrally the fascia does not extend to the outer wing margin.	Dorsally broad, white suffused with pink. Vein M3 not conspicuous across fascia. Ventrally the fascia does extend to the outer wing margin.
b) Orange submarginal band on the hindwings dorsally.	
Broad and conspicuous in both sexes but especially in females.	Reduced in the male, especially medially; distinct or occasionally reduced in the females.
c) Eyespots of hindwings dorsally. Anterior eye-spot normally one-fifth to one-third larger than posterior eye-spot.	Anterior eye-spot one-third larger to twice as large as posterior eye-spot.
d) Ventral coloration of hindwings. Basically dull grey to dark brown with maculations and submarginal eye-spots largely obliterated by the ground color.	Basically brown with conspicuous maculations of variable intensity light brown to dark or reddish brown. Sub-marginal eye-spots usually distinct.
e) Coloration of antennae. Dark tawny or brown stem with black club.	Pale cream or white stem with a dark club.

character which can be used to identify mature living larvae. The bases of the mid-dorsal scoli of living *J. evarete* larvae are iridescent turquoise whereas those of *J. genoveva* larvae are iridescent purple. Larvae of both species have eight rows of scoli on the thoracic segments and nine longitudinal rows of scoli on the abdominal segments, including a mid-dorsal row that is absent on the thorax.

The pupae of *J. evarete* are consistently dark brown to dark grey with black markings on the wing cases and the abdomen, whereas the pupae of *J. genoveva* are variable, being grey-brown to light brown with pink, white and greenish markings.

Ecology and Distribution of the two Species

J. evarete occurs in and around mangroves and coastal scrub in Jamaica. Seven resident populations have been located along the south

coast: Holland Bay - Rocky Point, Lyssons, Yallahs, Palisadoes - Green Bay, Old Harbour Bay, Portland Point and Starve Gut Bay. Only one population has been located on the north coast just west of Falmouth. Occasional capture of individuals between these localities at certain times indicate that some dispersal occurs.

J. genoveva is essentially an insect of open grassland islandwide, but both species fly together where mangrove woodland borders on pastureland and along roads, clearings and paths through such woodland. No specimens which could be considered hybrids between the two species were seen, even where populations of the two were sympatric. Similarly, no evidence of hybridization was observed in any of the collections studied.

The only larval foodplant of *J. evarete* in Jamaica is Black Mangrove *Avicennia germinans* (L.) (*Avincenniaceae*) (= *A. nitida* hitherto classified in the Verbenaceae). Most larvae have been collected feeding on cotyledons of seedlings of this plant. Larvae have been collected at Holland Bay, Palisadoes and Green Bay in April, May, November, December and January, with larvae most abundant in December. The predominantly coastal distribution of this locally occurring insect may be explained by the distribution of the larval foodplant.

The known larval foodplants of *J. genoveva* in Jamaica are *Stachytarpheta jamaicensis* (L.) Vahl., *S. cayennensis* (Rich) Vahl. (Verbenaceae), *Ruella tuberosa* L., and *Blechum pyramidatum* (Lam) Urb., (Acanthaceae). These plants are widely distributed in grassland and along roadsides throughout Jamaica, especially at elevations below 700 m. One larva was collected feeding on the ornamental *Barleria cristata* L., (Acanthaceae). *Asystasia* (cultivated) and *Lippia* (wild) also occurs within this species habitat but have not been noted as larval foodplants, although these are recorded as foodplants elsewhere. Larvae have been collected islandwide in all months of the year except February and April and they are most abundant between July and September.

Larvae of *J. evarete* (instars one to five) would not feed on *Stachytarpheta jamaicensis*, *Ruella tuberosa* or *Blechum pyramidatum* in captivity nor would larvae of *J. genoveva* (instars one to five) accept *Avincennia germinans* as a foodplant.

Seasonal Variation in Adult Coloration

In both species there is a tendency for specimens that emerge from pupae between December and April to be darker in ground color, both dorsally and ventrally, than those emerging between May and November. Females of *J. evarete* that emerge between May and November are conspicuously lighter in ground color on both wing surfaces. Males and females of *J. genoveva* emerging between December and April are darker in basic coloration, especially those reared from localities above 500 m.

There may also be partial obliteration of the eyespots on the ventral surface of the hindwings. At no time during the year do all of the characters (see Table 1) separating *J. evarete* and *J. genoveva* become indistinct.

The pale fascia on the forewings of *J. genoveva* is occasionally completely suffused with pink (frequency 2.4% in Jamaica, n = 125). Any occurrence of this coloration in *J. evarete* would be obscured by the normally tawny ground color of the fascia in this species.

Behavioral Differences between Species

Males and females of *J. genoveva* may be observed flying together close to the ground in fields or along roadsides. Flight consists of a short series of powerful wing-beats, followed by a longer series of wing-beats of small amplitude resulting in a "scudding and planing" flight. Males of *J. evarete* are common along the edges of mangroves and appear to be more strongly territorial than those of *J. genoveva*. Females of *J. evarete* remain in the mangrove woodland for the most part but appear at the woodland's edge to feed or, in late afternoon, to rest on the ground in sunlit locations. Flight in both males and females of *J. evarete* consists of a long series of powerful wing-beats as the insect rises over shrubs and trees followed by weak gliding and fluttering as the insect descends to the ground again. Males exhibit "scudding and planing" flight over short distances but for both sexes flight is predominantly "soaring and fluttering".

Discussion

Forbes (1928), Carpenter and Lewis (1943), Munroe (1951) and Brown and Heineman (1972) considered that there was a single species of *Junonia (Precis)* in Jamaica. They noted two color forms, but because of similarities in the male genitalia most authors regarded these as seasonal forms.

By collecting both "color forms" throughout the year, it became apparent that each form remained morphologically distinct despite minor seasonal variations and that these forms, for the most part, occupied separate ecological habitats. A study of the male genitalia of a sample of each color form indicated that two populations of *Junonia* were present and subsequent examination of the chromosomes confirmed that these populations represented separate species. In addition there are differences between the two species in the larval foodplants, the immature and adult stages, and in adult behavior.

No hybridization was observed where these two species occur. Using Cramer's original description of *Junonia* species from Surinam (1779 & 1780) we have applied the names *J. genoveva* to the commonly occurring

species which is distributed all over Jamaica, and *J. evarete* to the less common species which is only locally abundant.

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Notes on *Caligo memnon* Felder and *Caligo atreus* Kollar (Lepidoptera: Nymphalidae: Brassolinae) in Costa Rica and El Salvador

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Abstract. The life cycles and associated natural history for *Caligo memnon* Felder and *Caligo atreus* Kollar (Nymphalidae: Brassolinae) were studied in Costa Rica and El Salvador (the latter for *C. memnon* only). Brief, general descriptions of early stages are given as supplementary data to previously-published information on early stages, especially for *C. memnon* and much less so for the more elusive *C. atreus*. Preliminary field data on the relative abundance of both species at banana baits at one Costa Rican locality are also summarized. Both species display a variety of traits compatible with their life style of dwelling close to the ground in tropical forest habitats, including cryptic color patterns and behavior in both adults and caterpillars, and the feeding by adults on fallen fruits. *Caligo* females may have to mate more than once to fertilize all of their eggs, and males are attracted to electric lights. Major caterpillar food plant families in Central America are Musaceae and Maranthaceae, and our data suggests some divergence in food plants between these two species.

Introduction

". . .the great *Caligo*, with the owls' eyes on the under side of its wings, makes for the banana. . ."

> from: K. Guenther, 1927, *A Naturalist in Brazil,* London: G. Allen Ltd.

K. Guenther's remark constitutes one of the best known biological attributes of many brassolids, morphids, and satyrids in the American tropics, namely, the feeding association of the adult butterflies with fallen, rotten fruits such as bananas. Our paper calls attention to some life cycle and natural history features for the butterflies *Caligo memnon*

Felder and *Caligo atreus* Kollar (Lepidoptera: Nymphalidae: Bras-
solidae) as studied in Costa Rica (both species) and El Salvador (*C.*
memnon only). We add to the observation and studies of *Caligo* biology
already conducted in Central and South America by a variety of workers
(e.g., Boudar, 1915; Davis, 1915; Bodkin, 1916; d'Almeida, 1922; De
Azevedo, 1923; Waterston, 1923; H. Fruhstorfer in Seitz, 1924; Clease,
1926; Hoffman 1933; Breyer, 1929; Bullock, 1959; Labrador, 1961; Malo,
1961; Malo and Willis, 1961; Harrison, 1963; Tournier et al., 1966; Condie,
1976; Casagrande, 1979a, b, c, d; DeVries, 1983). Our paper provides a
first description of larval food plant and early stages for *C. atreus* as well
as new behavioral data for *C. memnon*, a widespread Central American
species (Seitz, 1924) well known for its occasional economic impact as a
defoliator of bananas (*Musa* sp., Musaceae) (Harrison, 1963). The early
stages of both species have also been described by Condie (1976).

Materials and Methods

In Costa Rica, larval *C. atreus* Koll. was studied at "Bajo la Hondura," a rugged
montane rain forest site near Coronado (9°03'N, 83°39'W), San Jose Province,
during June-August 1973. The complete life cycle of *C. memnon* in Costa Rica was
studied at the "Barranca Site," a tract of semi-deciduous lowland tropical forest
near Puntarenas (9°58'N, 84°50'W), Puntarenas Province, during August-
September 1973). In addition, adult behavior in both species was studied at
"Cuesta Angel," a montane rain forest site (about 1100 m elev.) near Cariblanco
(10°16'N, 84°10'W), Heredia Province, and at "Finca La Tigra," a premontane
tropical rain forest site (about 220 m elev.) near La Virgen (10°23'N, 84°07'W),
Heredia Province. Both sites were visited intermittently for one to five days be-
tween 1974 and 1983 for the purpose of observing sex ratios of butterflies at rotting
banana fruit bait placed in one or more piles on the ground at the edge of primary or
mixed advanced secondary-primary growth rain forest.

Adults of these species are easy to distinguish in the field by their very distinctive
wing-color patterns, both dorsally and ventrally (Fig. 1). Life cycle studies of *C.*
memnon in Costa Rica were limited to the Barranca Site (Fig. 2), even though this
species, and a closely related one, *C. eurilochus* Cramer, are widespread
throughout the country. And although *C. atreus* is also common in Costa Rica,
observations on the larval stage and pupation were limited to material discovered
at the rugged, often mist-shrouded Bajo la Hondura site (Fig. 3). The Costa Rican
field work was confined to one of us (A.M.Y.) while the other of us (A.M.) studied
C. memnon at various localities in the San Salvador area of El Salvador over
several years, and with assistance from other members of his family. *Caligo* is
generally rare in El Salvador, and observations on *C. memnon* there were limited
largely to culturing adults in an enclosed courtyard in Lomas Verdes. Observations
were made, however, on the general occurrence of *C. memnon* in the country, and
associated habitats. Adult feeding behavior relative to that of other brassolids was
also studied. These observations included surveying the abundance of adults of
both species at two piles of rotting bananas (approx. 40 bananas per pile) placed in
the same two forest-floor sites at "Finca La Tigra" over several years. These baits
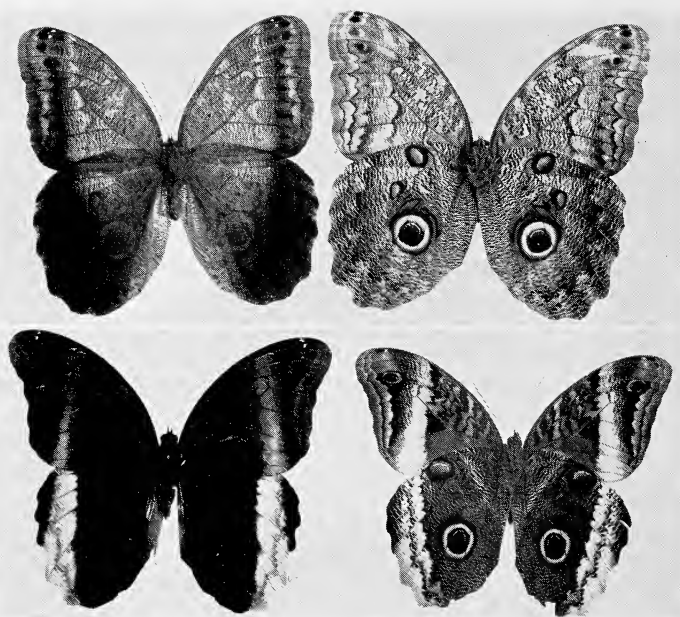
Fig. 1.   Adult *Caligo memnon* above, dorsal and ventral aspects; *Caligo atreus* below. From Costa Rica.

were visited several times of the day beginning on the day after they were set out.

In doing so, it was possible to obtain data on the relative number of butterfly "sightings" on a given date for both species.

In the Costa Rican studies, eggs and/or larvae were confined to large clear plastic bags containing fresh cuttings of the food plants. The bags were kept tightly closed and notes were taken on the appearance and behavior of individual life stages. Such observations complemented field observations of larvae on food plants in the wild. We generally followed the same methodology used to conduct similar studies on other brassolids, such as *Opsiphanes* (see Young and Muyshondt, 1975).

Results

Larval Food Plants.   In El Salvador, *C. memnon* uses several Musaceae as larval food plants: *Musa* spp., at the Barranca Site, *H. latispatha*. The larval food plants of *C. memnon* in both countries completely overlap those of *Opsiphanes tamarindi sikyon* Fruhstorfer (Young and Muyshondt, 1975). In both countries, *C. memnon* is found from sea level to about 1300 m elev., although the butterfly is far more abundant locally in Costa Rica. It shares with *C. atreus* and *C. eurilochus* the habit of thriving in shaded forest habitats, which, in most of El Salvador, are quite scarce. In Costa Rica, many Musaceae, particularly *Heliconia* species, are widespread and abundant in forest habitats at various elevations (see Daniels and Stiles, 1979). *Caligo* probably exploits various Maranthaceae as larval food plants,

Fig. 2.   Barranca Site locality in northwestern Costa Rica where *C. memnon* life cycle was studied. From top to bottom: overview of locality, forest habitat, and *Heliconia latispatha* larval food plant.

Fig. 3.   Bajo la Hondura locality in Costa Rica where *C. atreus* caterpillars were
discovered. Top: overview of rain forest ravine where this butterfly
thrives, and below: foot trail in forest where *C. atreus* caterpillars were
found on well-shaded *Heliconia* sp. plants.

particularly in Costa Rica where more forest is available, as these are known food plants for South American species (Casagrande, 1979a and associated references on early studies in South America). H. Fruhstorfer in Seitz (1924) suggests that larvae of many species feed interchangeably on Musaceae and Maranthaceae, closely allied taxa within the Zingiberales (Cronquist, 1968). Condie (1976) reared *C. memnon* on both *Heliconia* and *Canna* (Cannaceae) and *C. atreus* on *Calathea* (Maranthaceae) in Costa Rica, after discovering eggs on these plants in the field. The apparently wide regional distribution of individual species of *Heliconia* in Costa Rica, such as *H. latispatha* which is abundant in forests on both the Atlantic and Pacific slopes of the Central Cordillera from sea level to about 1600 meters elevation (Standley, 1937) as well as being widespread throughout much of Central America and northern South America, accounts for the widespread distribution of *Caligo* and other Brassolidae.

At Bajo la Hondura, *C. atreus* larvae were discovered on an unidentified species of *Heliconia* growing along a forest trail. There was a clump of four plants with leaves up to about three meters high and in the dense shade to one side of the trail (Fig. 3).

We have not found *Caligo* on any palmaceous plants in Costa Rica and El Salvador, even though such plants are sometimes exploited by the larvae of other Brassolidae (see Young, 1977, 1983; Young and Muyshondt, 1975). We suspect that *C. memnon* and *C. atreus* in Costa Rica may overlap considerably in the *Heliconia* species exploited as larval food plants (see also Condie, 1976), since both butterfly species are sympatric over a wide elevation. Although *C. memnon* and the very closely related *C. eurilochus* are well known defoliators of banana plants in commercial plantations in Central and South America (e.g., Boudar, 1915; De Azevedo, 1923; Malo, 1961; Malo and Willis, 1961; Harrison, 1963; Tournier et al., 1966), *C. atreus* is not generally considered as a pest species. The introduction into Costa Rica and other parts of Central America of commercial banana species from the Old World tropics in the late 1800s, such as *Musa paradisiaca* ("platano") and *M. sapientium* (Standley, 1937), may have led to a shift in larval food plants for some *Caligo* species (such as *C. memnon*) associated with *Heliconia* and Maranthaceae, and not others (such as *C. atreus*).

Early Stages. Harrison (1963) and Casagrande (1979a, b, c, d) give detailed descriptions of the early stages for *Caligo beltrao* Illiger and *C. memnon*. Because the early stages of *C. beltrao* probably typify those of most *Caligo*, the details for *C. memnon* are not given here. For *C. atreus* we have only partial data, namely, for fifth-instar larva and pupa only. We therefore emphasize the final instar larva and pupa of *C. atreus* relative to those of *C. memnon*, for which information is available (e.g., Harrison, 1963).

Harrison (1963) describes, without figures, all stages of *C. memnon*. We therefore have included illustrations of eggs and first three instars of larvae for this species (Fig. 4), eggs, first, from the Barranca Site in Costa Rica, the fifth-instar larva (Fig. 5), and prepupa and pupa (Fig. 6). The following details of the early stages were not reported by Harrison.

The cream-colored spherical and vertically-ribbed egg (about 1.7 mm dia.) turns reddish within a day of hatching, then darkens a few hours prior to hatching. While still cream-colored, a very thin brown line forms almost equatorially on the egg. Body color of the third-instar larva dull light green, the dorsal and medial oval

spots (Fig. 4) ringed with black and lavendar in the middle, with white posteriad. The anterior of oval spot has a tuft of black setae (on the sixth segment) and a second, much smaller tuft at end of the seventh segment. End of eighth segment with tiny dorsal spot of red. First thoracic segment mottled in white and brown, second one with small dorsal, medial patch of red with a white spot inside of it. Third thoracic segment devoid of conspicuous markings. Head capsule banded with stripes of tan and dark brown. Both head capsule and body covered, particularly laterally, with fine covering of very short white setae. Long white setae adorn four protuberances from the dorsal and lateral areas of the head capsule (Fig. 4).

Body ground color in fifth-instar larva (Fig. 5) light brown; conspicuous dorsal medial stripe dark brown. Dorsal oval patch on third abdominal segment orange with a thin brown line in center that does not reah posterior end of patch. Anteriorly this line fuses with a tuft of dark brown setae at edge of second abdominal segment. Posterior edge of fourth abdominal segment with very small orange spot with a tiny tuft of setae. A similar tuft appears at posterior edge of fifth abdominal segment. Various angular lines and markings of grainy brown spots radiate out from medial longitudinal body stripe. On thoracic segments stripe thickens and fills with shades of light tan. The tail forks of fifth-instar larva of *C. memnon* are about 10 mm long and covered generously with long light-tan setae (Fig. 5). A whitish-yellow line runs lengthwise through spiracular region and spiracles are ringed in reddish-brown. Ventrally body is dark purple and covered with many small setae giving it a brownish sheen.

The head capsule of the fifth instar striped similarly to that of previous instars and arrangement and sizes of the four prominent tubercles immediately separates this species from *C. atreus*. The dorsal-most pair of tubercles are longest, being about four mm long and with many long white setae at tips; lower half of these tubercles dark brown. The remaining three pairs progressively shorter but similarly colored and covered with setae. Length of these remaining pairs of tubercles (there are a total of four pairs) decreases as follows: subdorsal set: 2 mm long, lateral set: 1 mm long, and sub-lateral set: 0.5 mm long. Mandibles light brown. Ventrally eversible "neck" gland found just anterior to first pair of legs; gland is reddish, and present in all instars. It is similar to the same gland found in *Morpho* larvae (Morphidae).

Pupa (Fig. 6) warrants more detailed description than given in Harrison (1963). Pupa, 43 mm long by 21 mm wide (dorsal-ventral axis, through wing pads), mottled in various shades of brown and strongly angular on either side of thorax (Fig. 6). Cremaster beige, with faint brown line immediately ventral to the orange spiracle markings. Abdominal area with faint oblique stripe pattern of alternating shades of browns and yellows, but effect is not nearly as pronounced as in *C. atreus*. Wing pads resemble dried, dead leaves in appearance, but each forewing case bears triangular and convex silver spot along trailing edge, and second but tiny one immediately adjacent to larger spot (Fig. 6). Silver spots on wing pads in *C. memnon* pupae are not so pronounced as those found on *C. atreus* pupae. A conspicuous feature that immediately separates pupae of *C. memnon* from those of *C. atreus* is presence of distinct groups of stout bristles seen in former species and not in latter: All of these bristles originate from the ventral medial area of abdomen, and they are distributed as follows (Fig. 6): Abdominal segment 1: 10 bristles, central and scattered; segment 2: six bristles, central and scattered; segment 3: four
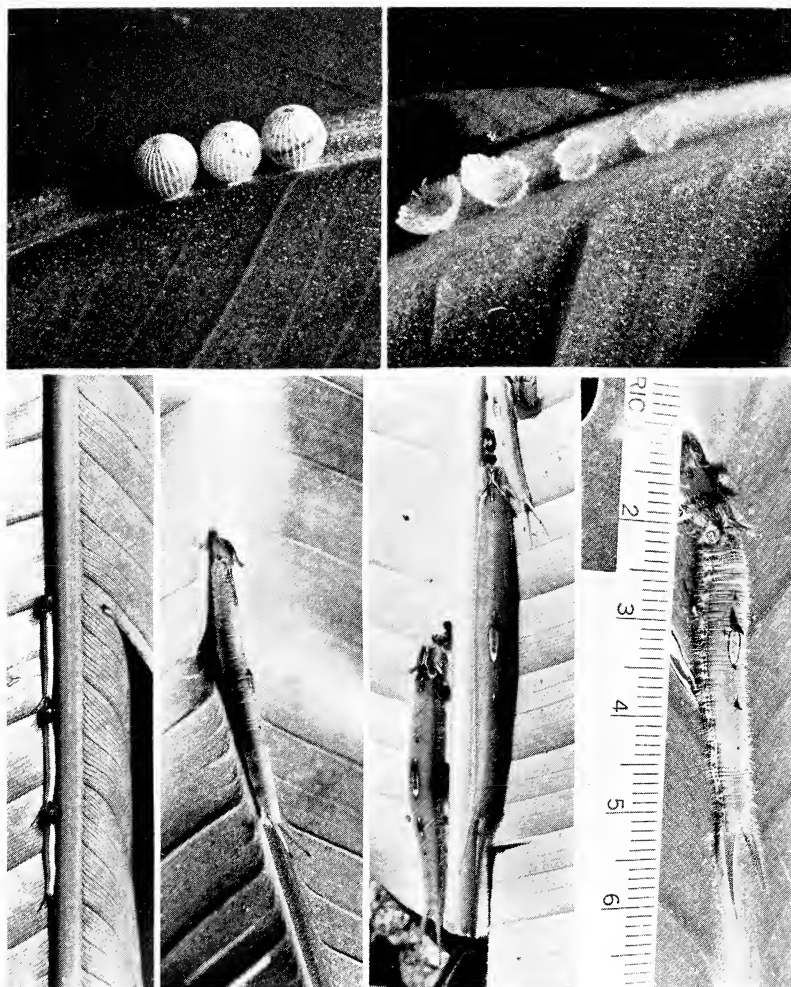
Fig. 4.   Early stages of *C. memnon* from Costa Rican studies. Clockwise, from upper left corner: triplet of eggs showing characteristic rings, partly-devoured egg shells, third, second, and first-instar caterpillars in typical resting positions on ventral sides of leaves of *Heliconia* sp. plants. Note group behavior of first-instar caterpillars (lower left).

bristles, central ad scattered; segment 5: two rows of many bristles; segment 6: two rows of approximately 50 bristles; segment 7: small, tight central cluster of less than 10 bristles. These bristles erect and black, and do not appear to have discernible tactile function. On dorsal area of head two additional clusters of bristles on each side; each cluster consists of two rows of approximately 25 bristles in all. These rows extend over area of the compound eyes and down underneath them. In
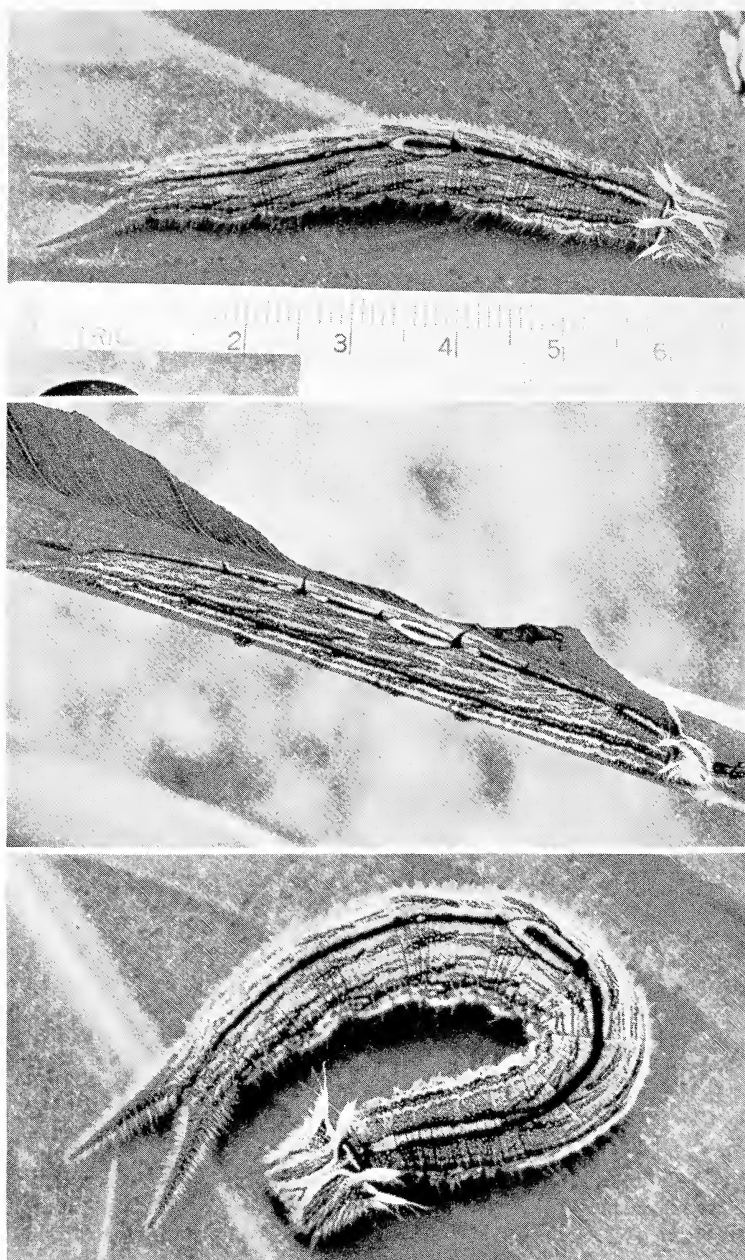
Fig. 5.   Fifth-instar caterpillar of *C. memnon*: dorsal (top), lateral (middle) and head capsule (below) aspects.

Fig. 6. Pupa (chrysalis) of *C. memnon* and pupation behavior: from left to right: prepupa, pupa-lateral aspect, and pupa-dorsal aspect. Note positions of groups of stout bristles clearly visible in the lateral view of the pupa. These bristles are absent in *C. atreus*.

central area of head dorsally another row of bristles, and a few of these extend ventrally.

Pupa results from molting of a prepupa that remains motionless for at least one day prior to molt (Fig. 6). When prepupa is deliberately disturbed, it everts ventral neck gland very quickly, although no noticeable odor detectable. Prepupa (Fig. 6) is light greenish-brown with a yellow hue. Although Harrison (1963) reports a pupal stage of 11-14 days, in our studies the pupa of *C. memnon* lasted 20 days under varying temperature and humidity conditions associated with rearing in Costa Rica. We reared a total of eight larvae, and without mortality. *Caligo* species are generally hardy enough for mass laboratory rearing associated with other kinds of research studies (e.g., Wasserthal and Wasserthal, 1980).

Fifth-instar larva of *C. atreus* generally much darker in overall body coloration (Fig. 7) allowing it to blend with shaded and subdued hues of petioles of *Heliconia* fronds on which they rest during daylight hours. The initial discovery of two *C. atreus* larvae, one on each of two different *Heliconia* plants about 20 meters apart, was greatly facilitated by the noticing of the ornate head capsules in patches of sunlight in the otherwise dark surroundings. The discovery was made at about 1400 hours on 26 June 1973 at Bajo la Hondura at a time when prevailing weather conditions were unusually sunny.

Fifth-instar larva of *C. atreus* measures 113 mm long by 12 mm at thickest (mid-section) region of body at time it stops eating in preparation for pupation. Tall "forks" are eight mm long and head capsule width is 6.5 m. There are five sets of tufts of long setae distributed lengthwise along dorsal medial line of body in following manner: Abdominal segment 3: 4 mm long; segment 4: 0.5 mm long; segment 5:
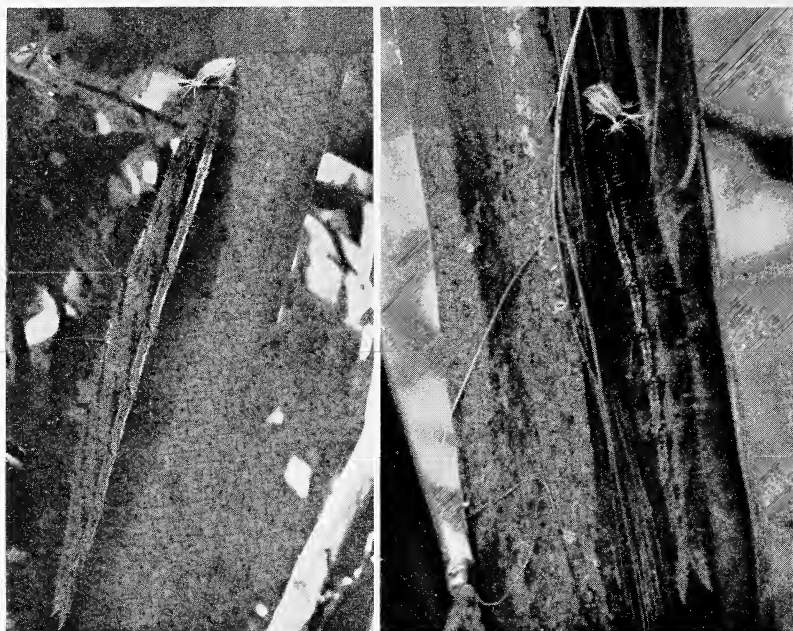
Fig. 7.   Fifth-instar caterpillar of *C. atreus* on *Heliconia* at Bajo la Hondura. Shown are typical resting positions of the cryptically-colored caterpillars on the well-shaded stems of the larval food plant; caterpillars almost concealed save for light highlighting the head capsules.

5.5 mm long; segment 6: 6.2 mm long, segment 7: 1 mm long. Dorsal-most protuberances of head capsule (Fig. 8) exhibit a strong "right-angle" bend or curvature, with apical half facing outward to one side of head capsule. Apical portion of each of these dorsal protuberances appears "swollen" in size relative to stem portion, and bears many long, filamentous white setae (Fig. 8). Remaining pairs of tubercles much smaller, straight in appearance and bear setae. Head capsule is basically tan with several dark brown vertical stripes, and posterior edge chocolate brown, a color extending into posterior sides of the large dorsal protuberances. Frontally all tubercles tan, although stem areas of most dorsal ones reddish-brown. Chocolate-brown coloration of posterior region of dorsal-most tubercles extends straight down side of head capsule as a thick brown stripe. Frontal plates of head capsule streaked vertically with thin lines of dark brown on otherwise tan or beige background color.

Above spiracles body mottled olive green hue with irregular blotches of dark brown. Three thoracic segments green with distinct dorsal-medial grayish-tan line. Dark brown "mottling" on remaining body segments (Fig. 8) forms series of inverted "W" patterns most evident looking down on larva directly from above. Apex of several of these "W" markings with tufts of compacted setae. These markings most prominent on abdominal segments four and five, and become faint near either end of body. Thin line of red faintly bordered in white and white speck-

ling runs through spiracle region on either side of body. Ventrally body cuticle and prolegs red. Sparse covering of short orange setae blankets most of body dorsally. Thoracic spiracles thickly ringed in brown which extends out posteriorly from each, disrupting the thin white line runing lengthwise through spiracle region (see above). Anteriorly-deflected tufts of long, compacted setae orange-brown near the base and black at tips. Eversible gland located ventrally just anterior to first pair of true legs pinkish and not red as in *C. memnon*.

Stout pupa (Fig. 9) 48 mm long by 20 mm (side to side, through the thoracic area), and patterned in shades of brown and deep yellow. Dorsal-ventral thickness through thorax is about 14 mm, and about 13 mm through abdomen. Oblique stripe pattern of dark brown lines on a yellowish background color most evident in abdominal region (Fig. 9), and silvery spots on wing pads far more prominent and convex in this species as compared with *C. memnon* (Fig. 9). Noticeably absent are several sets of rigid black bristles noted for pupa of *C. memnon*. Initially silvery, spot pattern on wing pads becomes golden within five days following pupation. Within a day of eclosion, pupa darkens noticeably, beginning in wing pads (Fig. 9), and eclosion is rapid, being completed within five minutes (Fig. 9). Terminal five segments of abdominal region capable of rapid, often violent, movements, and move freely from rest of pupa upon disturbance. "Cleft" noticeable between fourth and fifth abdominal segments where this articulation occurs; it is not noticeable in *C. memnon*. Duration of the pupa was 21 days.

Behavior of Caterpillars. Various authors (e.g., H. Fruhstorfer in Seitz, 1924; Harrison, 1963; Casagrande, 1979a) have described the nocturnal and crepuscular feeding habits of *Caligo* caterpillars, and the ability of caterpillars to spin silken resting mats and pathways to and from feeding sites on the food plants. We confirm these patterns of behavior within *C. memnon* and *C. atreus*. The caterpillars of both species anchor themselves, in all instars, in silken mats on the ventral, dorsal sides of leaves, as well as on the petioles of leaves. We interpret this behavior as part of crypsis, allowing the caterpillar to anchor itself securely at those times of the day and night when it is not feeding. Younger instars generally rest on the leaves proper, and the aggregative behavior of early instars in *C. memnon* (see Fig. 4) is well known (Harrison, 1963). Casagrande (1979a) describes in some detail the gregarious resting behavior in *C. beltrao* caterpillars in various instars. She also noted that when disturbed, caterpillars as a group will wave the head and anterior body segments back and forth. We have observed similar movements in *C. memnon* and *C. atreus*, and caterpillars evert the gland located in the "neck" region at such times. Harrison (1963) noted that sometimes as many as 12 young caterpillars of *C. memnon* comprise a group, and that group size generally diminishes as caterpillars get larger in size. During the fifth instar, for example, usually the caterpillar occurs singly on the food plant, or in groups of two or three (Harrison, 1963). In our studies, we have noticed that first-instar *C. memnon* rest head-to-head along the midrib on the ventral surface of a *Heliconia* leaf. First-instars build silken trails to the edge of the same leaf and feed there in group fashion. Later instars, such as the second and third-instars, exhibit similar resting and feeding behavior on the leaves. When we lay on the ground on our backs and look up through a *Heliconia* leaf having one or more caterpillars on the ventral surface, the insects are practically indistinguishable from the general color of the leaf. But when we turn the same leaf over and look down at the caterpillars, they are very obvious. We suspect, therefore, that the caterpillars of *Caligo* have evolved a form of crypsis most
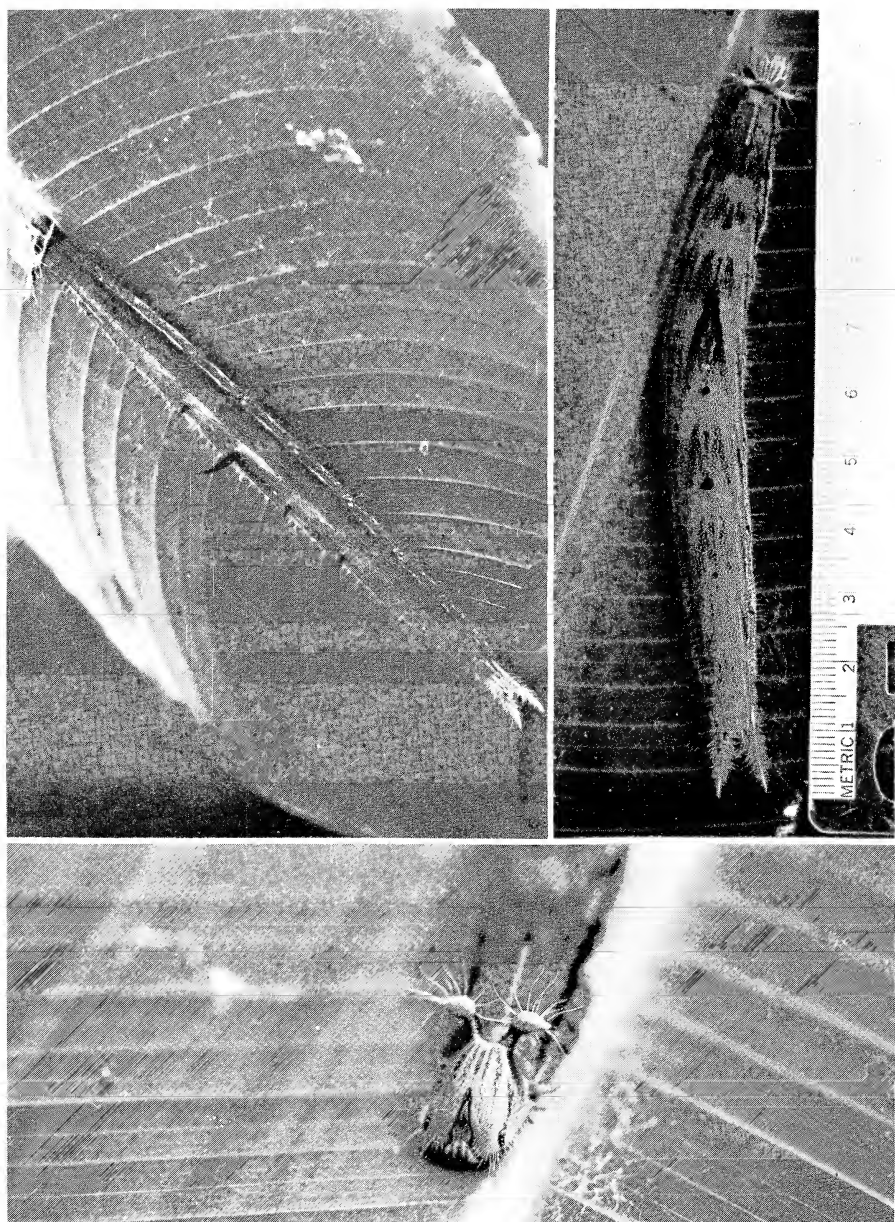
Fig. 8.   Fifth-instar caterpillar of *C. atreus*, emphasizing dorsal (upper two photos) and head capsule (below) details.
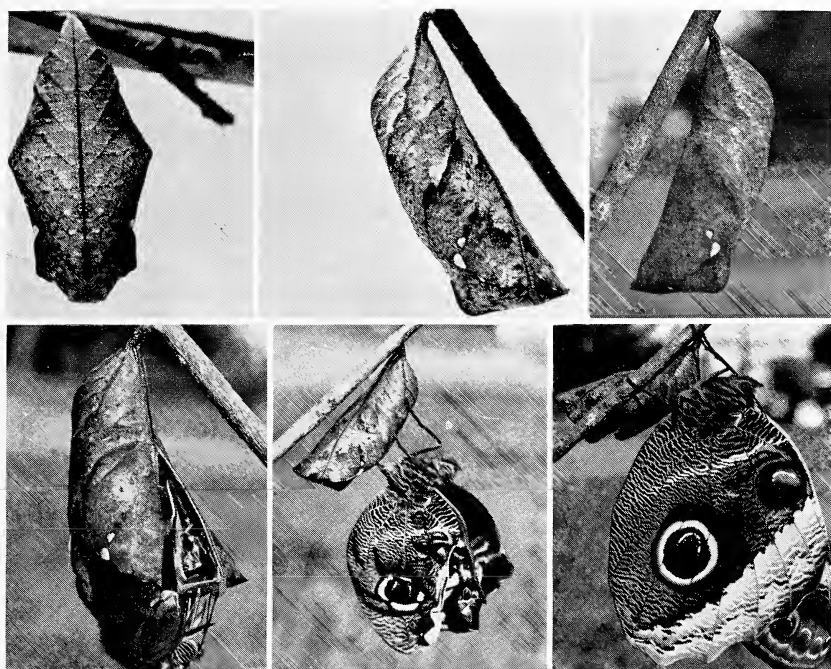
Fig. 9. Pupa (chrysalis) of *C. atreus*, and adult emergence. Note conspicuous silvery-gold spots on wing cases and banding color pattern of abdomen.

applicable to ground-foraging insectivorous and omnivorous predators, ones that look up to the undersides of leaves for their prey.

The more brownish hues of the fifth-instar are adaptations for being cryptic on the similarly colored petioles and trunk areas of *Heliconia* plants in shaded forest habitats, as the caterpillars move to such resting places when they are larger in size. Occasionally, at Cuesta Angel in Costa Rica, one of us (A.M.Y.) has even seen *Caligo* fifth-instars resting on non-food plants adjacent to *Heliconia* plants during the daylight hours.

We have noticed that first-instar caterpillars often rest near vacated egg shells soon after hatching, and that they devour egg shells to varying degrees (see Fig. 4). Egg shells are often only partly eaten.

Hymenopterous parasites are reported in the literature to take heavy tolls on the eggs of *Caligo* species in the wild (e.g., Waterston, 1923; Malo, 1961; Malo and Willis, 1961), including *C. memnon* in Costa Rica (Harrison, 1963). We have not found high levels of such egg parasitism in our studies. In El Salvador, the caterpillars of *C. memnon* are quite susceptible to parasitism by tachinids and we found only one instance of a braconid wasp larva in a caterpillar of this species. Harrison (1963) reports dipterous parasitism on the pupa of *C. memnon* in Costa Rica. Condie (1976) discovered that eggs of *C. memnon* are attacked by *Oencyrtes* sp. (Hymenoptera: Encrytidae) and larvae by *Winthemia pinguis* (F.) (Diptera:

Tachinidae) in Costa Rica.

In our experience, *Caligo* shares with *Eryphanis* (Brassolidae) and *Morpho* (Morphidae) the behavioral characteristic of resting on the trunk of the larval food plant during the fifth-instar period, a time when the appearance of the caterpillar in all three genera changes dramatically to a mottled brown general color (see also Young and Muyshondt, 1973). The caterpillars of these genera also share in common the presence of the eversible ventral gland in the "neck" region behind the head capsule. This structure is absent in the brassolid genus *Opsiphanes* (Young and Muyshondt, 1975) as well as "suspect" satyrid genera such as *Tisiphone (Manataria)*. In *Morpho* the gland, when everted, produces a noticeable rancid margarine-like odor, but such an odor has not been noticed in *Caligo*. The gland is also absent in *Narope ayllastros testaceae* Godman & Salvin (Brassolidae). Whether or not such a gland is defensive in function, or serves to coordinate group behavior in earlier instars, remains to be studied. The strongly nocturnal or crepuscular feeding habits of various larval instars in *C. memnon*, and presumably in *C. atreus*, suggests that the caterpillars are subject to attack by visually-hunting diurnally-active predators.

Behavior of Adults. Various reports, and the present study, indicate that adult *Caligo* butterflies are very crepuscular in their flight activities (e.g., Seitz, 1924; Young, 1972). By observing butterflies on rotting fruit baits (primarily bananas) distributed in piles on the ground cover of premontane rain forest ("Finca La Tigra") and montane rain forest (Cuesta Angel) over several years, the sex ratio of butterflies on such baits is heavily skewed towards males for both *C. memnon* and *C. atreus*. During hot, dry days, such as during the period January-March at such localities, densities of *Caligo* adults at fruit baits increase two or three-fold, a phenomenon we suspect is related to greater moisture stress on these insects. Densities are lowest, in the Costa Rica studies, at the height of the rainy season (July-August). We have no explanations for the apparent temporal changes in abundance of both species at baits in the same forest habitat over the year (Table 1). Other researchers, however, have noted marked cycles of abundance in the Brassolidae in South America (Brown, 1972). The Costa Rican studies (see also Young, 1972) indicate that *Caligo* adults feed on a broad range of rotting fruits, including pineapple, mango and banana. On rainy, overcast days, it is not uncommon to find *C. memnon* adults in particular at fruit baits on forest floors in Costa Rica; otherwise, the daily feeding patterns are very crepuscular, and there is a strong early morning peak of feeding between 0630 and 0800 hours on sunny days. At the Barranca Site, densities of *C. memnon* are very high during the first half of the long dry season of this region, and between 5-20 individuals of this species can be found on a single pile of bait (about 30 cm diameter) between 0700 and 1000 hours. During the latter half of the dry season, densities decline markedly, presumably the result of increased adult mortality and lack of adult recruitment during this period (see Young and Thomason, 1974, for discussion of a similar pattern of dry season population decline in *Morpho peleides* Kollar at this locality).

Interesting to us is the almost exclusive association of *Caligo* adults with fallen fruits as food sources, in contrast with other fruit-feeding Neotropical butterflies. In El Salvador, for example, *Opsiphanes cassina fabricii, Archaeoprepona demophron* Fruhstorfer, *Historus odius* Fabricius, *Smyrna blomfildia* Fruhstorfer, *Colobura dirce* Linnaeus, and others feed on fruits still on trees. The feeding by

these adult butterflies occurs shortly after the hanging fruits are pierced and wounded by the scarabeid beetle *Cotinis mutabilis*: the butterflies feed at the fleshy entrance hole made by the beetles as the latter feed inside the fruit. When the beetles exit later, the butterflies fly off and return shortly thereafter. This arboreal fruit-feeding behavior in these nymphalids and brassolids has been noted for various species of *Citrus* as well as breadfruit, *Artocarpus communis*, introduced into El Salvador from the Pacific Islands. *Caligo, Eryphanis, Narope,* and *Manataria*, however, exhibit only ground-level feeding on fallen fruit. Further-more, we note that most Brassolidae perch lower down in the vegetation than do most Nymphalidae; the highest perching forms include *Smyrna, Colobura, Anaea* and *Prepona*; "intermediate" level perching forms include *Opsiphanes*; the lowest perching forms are those genera mentioned above as well as satyrids such as *Taygetis* sp. While the Brassolidae perch primarily on the trunks of trees, most Morphidae and Satyridae perch on leaves.

Two female *C. memnon* confined to a small courtyard with banana trees pro-duced a total of 165 eggs, with one female living in this outdoor cage for three weeks, and the other one for 18 days. The eggs were discovered as clusters of three to eight eggs, each cluster arranged as an irregular line on the borders or undersides of leaves; no eggs were found on other parts of the banana trees. Adults fed ade-quately on rotten bananas. The last 30-40 eggs produced jointly by one of the but-terflies proved to be infertile, suggesting that female *C. memnon* may need to copulate more than once to fertilize all of the eggs produced in her reproductive life span. Although there was an abundance of banana and *Heliconia* plants in a nearby ravine less than 50 meters away from the courtyard, no male *C. memnon* were attracted into the area. Yet male *C. memnon* were commonly seen at electric street lights in this area at night. Perhaps courtship requires visual contact be-tween the sexes, even though the abdominal scent organs of male *Caligo* are well known (Figs. 10-11). The courtship scent system of *Caligo* has been considered as an evolutionary link of this genus with "suspect satyrids" such as *Bia* and *Manataria*, which have similar structures (Richard I. Vane-Wright, pers. comm.). The arrangement and functioning of the glandular plates of male *Caligo* (Fig. 10) and associated wing hairs (Fig. 11) have been discussed elsewhere (Barth, 1954; Casagrande, 1979d).

In the Costa Rican field studies, one of us (A.M.Y.) also found triplets of eggs placed on new leaf tips of *Heliconia* plants at the Barranca Site. One doublet of eggs was also found on the thick stem about 11 cm off the ground on a very small *Heliconia* plant. Triplets of *Caligo* eggs have also been found along the midrib on the dorsal surfaces of *Heliconia* leaves. In one oviposition act observed, a very tat-tered *C. memnon* was observed (29 June 1972) at 1745 hours in a light drizzle plac-ing two eggs on the ventral side of the frayed tip of a *Heliconia* leaf. The actual egg-placement behavior lasted several minutes.

Discussion

Our studies of two species of *Caligo* in Central America reveal little dif-ference in their basic natural history. In Costa Rica, both species, *C. mem-non* and *C. atreus,* are sympatric throughout the country, particularly in the lowland and premontane tropical wet forest sites associated with the
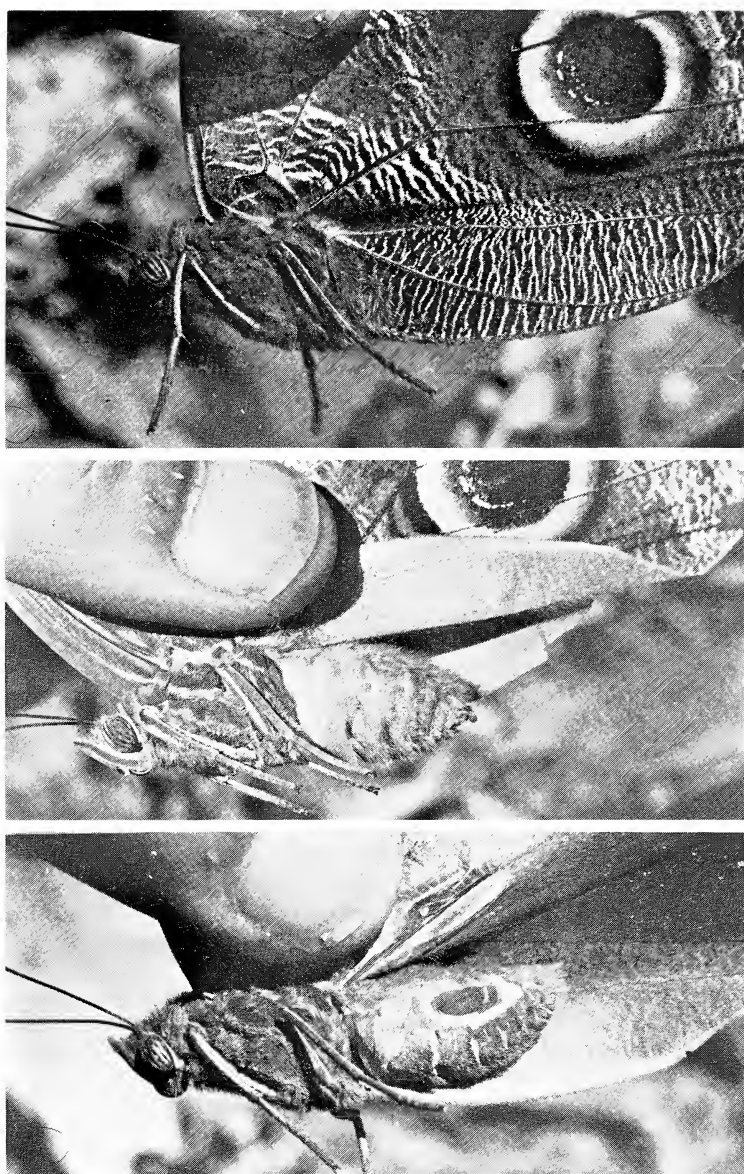
Fig. 10. Scent organ in male *C. memnon*. Top to bottom: concealment of
          abdominal area by hindwing in typical resting position, exposure of
          female abdomen, and exposure of male abdomen showing position of
          scent gland patches. At the Barranca Site in Costa Rica. Similar organ
          found in male *C. atreus*.
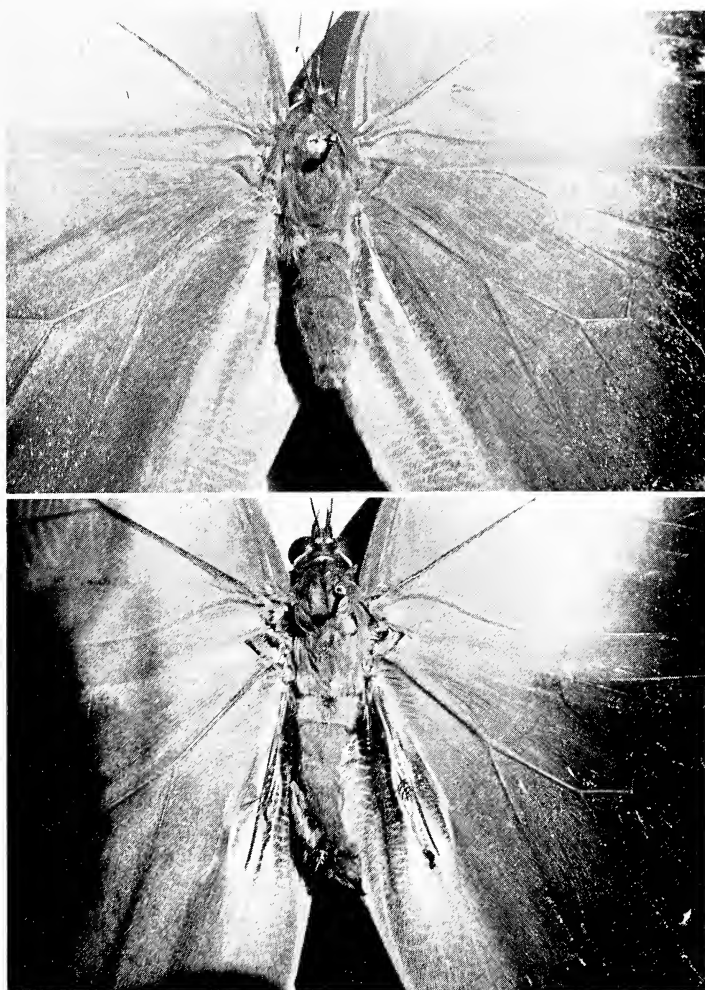
Fig. 11.   Scent hairs on hindwing in male *C. memnon* (below) and absence in female (above).

Atlantic watershed. Adult population densities at experimental fruit baits on forest floors suggest that neither species is very common, but that such densities may increase facultatively during the lengthy dry season of some areas, presumably in response to moisture stress in such habitats (i.e., there being fewer moist microhabitats per unit area of habitat). In El Salvador, *C. memnon* is the common species of the genus, whereas in Costa Rica, three species in particular, *C. memnon, C. eurilochus,* and *C. atreus*, are the most familiar species in many regions. *Caligo atreus*

uranus, the form studied in Costa Rica, represents the most northern extension of *C. atreus* from South America, having a range in Central America through Honduras (Seitz, 1924). Prior to our report, there has been no published information on the early stages and larval food plant of *C. atreus*. In this context, it is interesting to note the very marked difference in the configuration of the head capsule protuberances between this species and those of others already described (see Davis, 1915; Seitz, 1924; Harrison, 1963; Casagrande, 1979a). We suggest that the head capsule of fifth-instar *C. atreus*, as well as the prominence of silvery-gold spots on the pupa, are species-specific diagnostic characteristics that distinguish this species, including *C. memon* and *C. beltrao* (Casagrande, 1979a). Furthermore, our studies, and those of others cited in this paper, suggest that different species of *Caligo* are fairly catholic in their larval food plant associations, with most species associated with various Musaceae and Maranthaceae.

The crepuscular feeding habits of both adults and caterpillars of *Caligo*, as well as the generally cryptic appearance of these life stages, reflect a strategy of crypsis or concealment from visually-hunting diurnally-active predators. Some studies (e.g., Malo, 1961; Malo and Willis, 1961; Harrison, 1963) suggest that the early stages of *Caligo* are parasitized heavily by hymenopterans, a pattern that contributes to the generally low abundance of these butterflies in nature. Outbreak conditions of some species such as *C. eurilochus* and *C. memnon* in banana plantations in Central and South America (Harrison, 1963; Tournier, 1966) represent unusual ecological conditions favoring large increases in the population densities of herbivorous insects associated with monoculture stands of a tropical crop. In fact, the deliberate introduction of bananas into Central America from the Old World tropics may have caused a significant change in the distribution and abundance of a species such as *C. memnon*, but with little or no effect on a strictly *Heliconia* and maranthaceous-associated species such as *C. atreus*.

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Table 1.   Presence of *Caligo* species on rotten banana baits* in advanced secondary and primary tropical rain forest in northeastern Costa Rica.

DATE	TIME	BUTTERFLIES PRESENT**
13 Nov. 1981	1300	none
14 Nov. 1981	1300	none
15 Nov. 1981	0830	*C. memnon* (2)
15 Nov. 1981	1400	none
4 March 1982	1200	*C. atreus* (1)
4 March 1982	1500	none
5 March 1982	0800	*C. memnon* (1); *C. atreus* (1)
5 March 1982	1200	none
5 March 1982	1500	none
5 March 1982	1700	none
6 March 1982	0800	*C. atreus* (1)
6 March 1982	1300	none
9-12 July 1982	0900	none
9-12 July 1982	1100	none
9-12 July 1982	1500	none
9-12 July 1982	1600	none
27-31 July 1982	0800	none

27-31 July 1982	1100	none
27-31 July 1982	1300	none
27-31 July 1982	1400	none
2 Dec. 1982	0645	*C. memnon* (1); *C. atreus* (1)
2 Dec. 1982	1400	none
3 Dec. 1982	0800	*C. memnon* (1)
3 Dec. 1982	1600	*C. memnon* (1)
4 Dec. 1982	0900	none
4 Dec. 1982	1000	none
4 Dec. 1982	1100	none
2 March 1983	1300	none
3 March 1983	1300	*C. memnon* (1); *C. atreus* (1)
3 March 1983	1700	*C. memnon* (2); *C. atreus* (2)
8 August 1983	0800	none
8 August 1983	1300	none
9 August 1983	0700	*C. atreus* (1)
9 August 1983	1100	none
9 August 1983	1400	*C. atreus* (1)
9-12 Nov. 1983	0800	none
9-12 Nov. 1983	1100	none
9-12 Nov. 1983	1400	none
9-12 Nov. 1983	1500	none
27-29 Feb. 1984	0900	none
3-4 Aug. 1984	1100	none
3-4 Aug. 1984	1500	none
3-4 Aug. 1984	1600	none
18 Feb. 1985	1100	none
18 Feb. 1985	1500	none
27 Feb. 1985	1200	none
27 Feb. 1985	1500	*C. memnon* (1)
28 Feb. 1985	0800	*C. memnon* (2); *C. atreus* (1)
28 Feb. 1985	0900	*C. memnon* (2)
28 Feb. 1985	1000	*C. memnon* (2); *C. atreus* (1)
28 Feb. 1985	1130	*C. memnon* (1)
28 Feb. 1985	1400	none
3 March 1985	0800	none
3 March 1985	1000	none
3 March 1984	1200	none
3 March 1985	1330	none
3 March 1985	1500	none

*Two piles of vinegary-smelling, rotten bananas, each approximately 0.5 m diameter and roughly 40 m apart, were placed on the ground in the same places for all censuses. Baits were distributed the day before butterfly observations began.

**Data here excludes sightings of other butterflies (e.g., *Morpho*). Figures in parentheses refer to numbers of individuals seen.

Habitat Associations of Wetland Butterflies Near the Glacial Maxima in Ohio, Indiana, and Michigan

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Abstract. Thirty-seven wetland complexes were analyzed and the habitat associations of 15 wetland butterfly species were determined. Species which are restricted to specific wetland types include *Oarisma poweshiek, Euphyes bimacula, Epidemia dorcas, Calephelis muticum, Neonympha mitchellii* (all bog fens), *Euphyes dukesi* (swamps), and *Charidryas harrisii* (sedge meadow). Species which are less restrictive in habits are *Poanes massasoit* (bog and prairie fens), *Poanes viator* (sedge meadows, bog fens, and swamps), *Euphyes dion* (sedge meadows and bog fens), *Euphyes conspicua* (sedge meadows, bog fens, and bogs), *Hyllolycaena hyllus* (marshes, sedge meadows, bog fens, prairie fens, and bogs), *Euphydryas phaeton* (sedge meadows, bog fens, and prairie fens), *Satyrodes eurydice* (sedge meadows, bog fens, prairie fens, and bogs), and *Satyrodes appalachia* (bog fens and swamps). Fens contain the most diverse butterfly assemblages of the wetland types considered. Only two species, *E. phaeton* and *H. hyllus,* occur in the poorly developed wetlands south of the glacial maxima.

Three ecologically segregated pairs of closely related species occur in the study areas (*S. eurydice-S. appalachia, E. dion-E. dukesi,* and *P. viator-P. massasoit*). These species pairs often coexist in the same wetland complexes but seldom interact due to differing habitat requirements.

Introduction

Wetland biological communities contain many of the rarest and most interesting plant and animal species native to the Great Lakes Region. Many plant species are restricted to these habitats because of strict soil or micro-habitat requirements, or because of reduced competition from weedy species within these habitats. These plants are often parasitized by insects which, like many parasites, are host specific and are thus also limited to wetlands.

Five basic types of wetland communities occur in Ohio, northeastern Indiana and southeastern Michigan (Curtis, 1959; Pringle, 1980). They are generally characterized as pioneer, now often relict communities that occur in isolated pockets of poor drainage and cool microclimate. Open wetlands represent communities which may have been characteristic of

plant associations adjacent to the retreating glacier. Wooded wetlands represent communities which replaced the pioneering communities as a result of natural habitat modifications. In addition to floristic differences, the community types generally differ in drainage patterns, soil types, and soil pH. The following descriptions describe those elements which are characteristic and therefore aid in the recognition of the various wetland types in their purest states. Many areas however, are mosiacs of wetland types and transitional communities are frequently encountered.

Marshes are the wettest of the habitats with water above the soil during much or all of the growing season. They often develop along streams and lake shores. The soil usually contains a high mineral content, even in areas where it superficially resembles organic muck. Typical plants are mostly herbaceous and include cattail (*Typha latifolia* L.), bulrush (*Scirpus validus* Vahl.), and occasionally blueflag (*Iris versicolor* L.).

Sedge meadows are similar to marshes and occur in the same situations, but are only seasonally flooded. The soils are usually sedge peat or organic muck. These wetlands are open communities dominated by sedges (*Carex spp.*) with scattered horsetails (*Equisetum spp.*), blueflag, and cattails.

Fens occur in depressions with impeded drainage in areas of calcareous substrates. They are generally found along streams or lake shores and are usually fed by springs. The soils are sedge peat and are neutral to highly alkaline. Two types of fens occur in the study area which differ primarily in the relict plant species present (Stuckey & Denny, 1981). **Bog fens** contain many plants of northern distributions such as pitcher-plant (*Sarracenia purpurea* L.), tamarack (*Larix laricina* [Du Roi]) and poison sumac (*Rhus vernax* L.). **Prairie fens** contain a significant number of prairie species, the most conspicuous of which is big blue-stem (*Andropogon gerardi* Vitman). Both types of fens contain extensive stands of sedges and shrubby cinquefoil (*Potentilla fruticosa* L.), and often contain lady slippers (*Cypripedium spp.*). Fens or parts thereof which are dominated by shrubs such as red-osier (*Cornus stolonifera* Michx) and willows (*Salix spp.*) are referred to as **carrs**. **Treed fens** are dominated by trees suich as tamarack, white cedar (*Thuja occidentalis* L.), or maples (*Acer spp.*). Because fens superficially resemble bogs, most named fens often contain the term.

Bogs are found in depressions, usually glacial kettle holes with completely impeded drainage. Bogs are fed by rain and ground water and there is often a remnant of open water in the center. The soil is sphagnum peat and is highly acidic. Bogs are dominated by mosses of the genus *Sphagnum* which form an almost complete ground cover usually obscured by taller plants. Ericaceous shrubs such as blueberries and cranberries (*Vaccinium spp.*) and leatherleaf (*Chamaedaphne calyculata* [L.]) form a conspicuous element in these habitats. Other distinctive plants include pitcherplant, cottongrasses (*Eriophorum spp.*), sundews

(*Drosera spp.*) and several orchids. **Wooded bogs** are dominated by tamarack with scattered poison sumac.

Swamps occur along streams and rivers and are seasonally or permanently flooded. Swamp soils are high in organic matter but are not peaty. They are dominated by trees such as willows, maples, buttonbush (*Cephalanthus occidentalis* L.), and red-osier. Herbaceous plants include various sedges and skunk cabbage (*Symplocarpus foetidus* [L.]).

The wetlands of the study area support 15 species of butterflies not typically encountered in other habitats. These butterflies and their hostplants must have invaded the region after the Wisconsin glaciation from refugia located somewhere south of the glacial boundary as habitats became available (about 15,000 B.P.). An east-west route may have existed from the Atlantic Coastal Plain to the Great Lakes region via the once flooded Mohawk Valley in New York (Peattie, 1922; Shapiro, 1970). Species which may have followed this route are *Neonympha mitchellii* French and *Euphyes bimacula* (Grote and Robinson). Alternately, the Mississippi Valley may have allowed invasion of the Great Lakes region from refugia located on the Gulf Coastal Plain. Probable butterfly examples include *Satyrodes eurydice* (Johansson) and *Calephelis muticum* McAlpine. Pollen profiles from several Great Lake Region sites indicate that this migration took place between 13,000 and 5,000 B.P. in the study area (Vesper and Stuckey, 1977). During the xerothermic period (about 5,000 B.P.), wetlands in these corridors may have been altered resulting in the extinction of many or all of the connecting populations between the refugia and the Great Lakes (Shapiro, 1970).

Materials and Methods

I sampled a total of 24 wetland complexes during the summers of 1982-1984 (Fig. 1, Table 1). The sites were chosen to be representative of the wetland types present throughout the study area. However, undisturbed areas were given priority over disrupted wetlands. Each wetland was sampled at least three times at two week intervals from late June through July to insure that the flight periods of all the wetland species were covered. All available habitats at each site were sampled as thoroughly as possible on each visit. Extensive field notes were taken concerning the habitats of each butterfly species encountered at every site.

Data from a few sites from within the study area are available in the literature and were incorporated unchanged (Albrecht, 1974; McAlpine *et al.*, 1960) or as a supplement to my own sampling (Badger, 1958; Price, 1970; Price & Shull, 1969; Palister, 1927). Specimens in the Ohio State University Museum and the Ohio Historical Society Collection were also examined and specimens with specific locality data were utilized to supplement my sampling. Additional data were solicited from several other collectors as noted in Table 1.

Sedges were identified with the keys in Braun (1967). However, the vast majority of the sedges were not in bloom and were thus not identifiable to species and were categorized simply as broad-leaved or narrow-leaved.
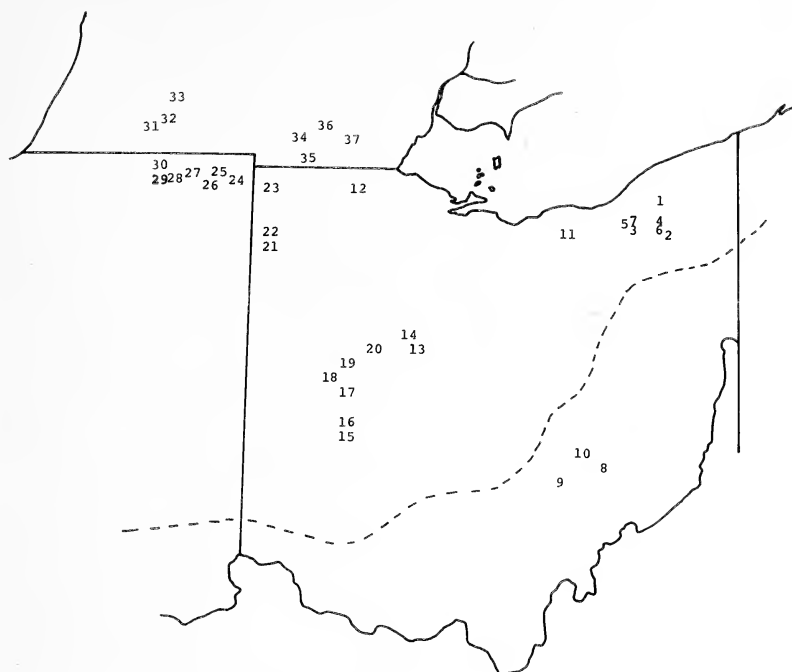
Fig. 1. Approximate locations of wetland complexes analyzed. Dashed line is
the Wisconsin glacial maxima. Numbers refer to site numbers in
Table 1.

Habitat utilization by *Poanes massasoit* (Scudder) and *P. viator* (Edwards) was
determined at Mud Lake in 1983. The fen was divided into seven sections which
reflect the limits of mat types as defined by Brodberg (1976) (Figure 2). The dis-
tribution of the two species within the fen was determined by walking the
perimeter and recording the location of each specimen sighted. The south-west
quarter of the fen was not censused because of the fragility of the mat. Seven cen-
suses were taken in July 19-24 between 1000 hrs and 1700 hrs (eastern standard
time). Allowing that some individuals may have been recorded more than once per
census, a 2x2 contingency table was utilized to analyze this data.

Results

Table 1 lists the sites included and records the different habitats pre-
sent at each site. All but three of these sites are located in glaciated areas
(Figure 1). Over half of the sites are fens which reflects the prevalence of
this type wetland throughout the study area. Bogs are absent over the
western portion of the study area and are represented by three sites in
northeastern Ohio. Nine sites are primarily swamps. Marshes and sedge
meadows usually occur in association with other wetland types and were
sampled in conjunction with the other sites. Many of the sites are briefly

Site No.	Site Name	Site Description
1	Fern Lake	1
2	Triangle Lake	1
3	Kent Bog	1
4	Eagle Creek	1
5	Herrick Preserve	1
6	Mantua	1
7	Gott Fen	1
8	The Plains	1
9	Crane Hollow	1
10	Rockbridge Bog	1
11	Findley State Pk.[a]	
12	Campbell Preserve	2
13	Marysville[b]	2
14	Broadway[b]	1
15	Redmond Fen	
16	Prairie Road Fen	2
17	Cedar Bog[c]	1
18	Liberty Fen	2
19	Urbana Raised Bog	1
20	Reams Woods	
21	Junction[d]	1
22	Paulding[d]	
23	Mud Lake[e]	3
24	Cemetary Lake	
25	Marsh Lake	3
26	Binkley Bog	3
27	Beaver Dam Lake	
28	East Mongo	
29	Nasby Fen	
30	Cedar Lake[fh]	
31	Wakelee Bog[dh]	
32	Three Rivers Res.	
33	Yankee Springs[d]	
34	Liberty Bog[d]	
35	Morenci	
36	Sharon Hollow[g]	
37	Milan[d]	

Table 1. Description of and wetland butterflies recorded from the wetland sites discussed. Site numbers refer to Figure 1. More detailed site descriptions are contained in: 1 - Herrick, 1974; 2 - Cusick and Troutman, 1978; and 3 - Lindsey, *et al.*, 1969. * - denotes the dominant habitat type at each wetland. x - denotes the presence of a habitat type or butterfly species at each wetland. Data from, supplemented from, or courtesy of: a. - L. Martin; b. - J. Calhoun; c. - Albrecht, 1974; d. - M. Neilsen; e. - Price, 1970; f. - Price and Shull, 1969; g. - McAlpine *et al.*, 1960; and h. - Badger, 1958.

Table 2. Wetland butterflies and their habitat associations as recorded in this study. See text for explanation of habitat types.

Species	Marsh	Sedge Meadow	Bog Fen	Prairie Fen	Carr	Treed Fen	Bog	Wooded Bog	Swamp
O. poweshiek			X		X				
P. massasoit		X	X	X					
P. viator		X	X			X			X
E. dion		X	X						
E. dukesi									X
E. conspicua		X	X		X		X		
E. bimacula			X						
H. hyllus	X	X	X	X	X		X		
E. dorcas			X		X				
C. muticum			X						
C. harrisii		X							
E. phaeton		X	X	X					
S. eurydice	X	X	X				X		
S. appalachia						X			X
N. mitchellii			X		X				

described in Herrick (1974), Cusick & Troutman (1978), and Lindsey *et al.* (1969) (Table 1).

Table 1 records the butterflies known from each wetland. *E. bimacula* was not recorded during my sampling, but the species is known from four sites included in this study. Two other species, *Oarisma poweshiek* (Parker) and *Charidryas harrisii* (Scudder) were recorded from only one site each. The remaining species were encountered with regularity in the appropriate habitats.

Table 2 summarizes the habitat associations of each species. Additional comments for three of the species are as follows:

Oarisma poweshiek — Although Opler (1984) records the habitat of this species as "native tall-grass prairie", McAlpine's (1972 [73]) and my observations indicate that it is closely associated with bog fen meadows or carrs in Michigan.

Poanes viator — Shading does not seem to be a factor in the micro-

distribution of *viator*, which is the only species which apparently breeds in both sunny and shady habitats.

Euphyes dukesi (Lindsey) — This species is strictly confined to swamps. At Marsh Lake (primarily a fen) it is restricted to a small swamp even though the presumed hostplant ranges abundantly into the adjacent treed fen.

Figure 2 summarizes the distributions of *Poanes massasoit* and *P. viator* at Mud Lake. A 2x2 contingency table for statistical independence is highly significant (Chi-square = 20.94, p <0.005). Although this test is not entirely appropriate, the high significance indicates the high degree of disassociation between these species.

Discussion

Although the term fen is in general botanical usage, I have never encountered it in reference to North American butterfly habitats even though most references to bogs actually refer to fens (e.g. Albrecht, 1974; McAlpine, *et al.*, 1960; Price, 1970; Price & Shull, 1969; Badger, 1958). Fens in fact support the most diverse butterfly assemblages of the wetland types discussed. The resulting confusion has obscured many important relationships.
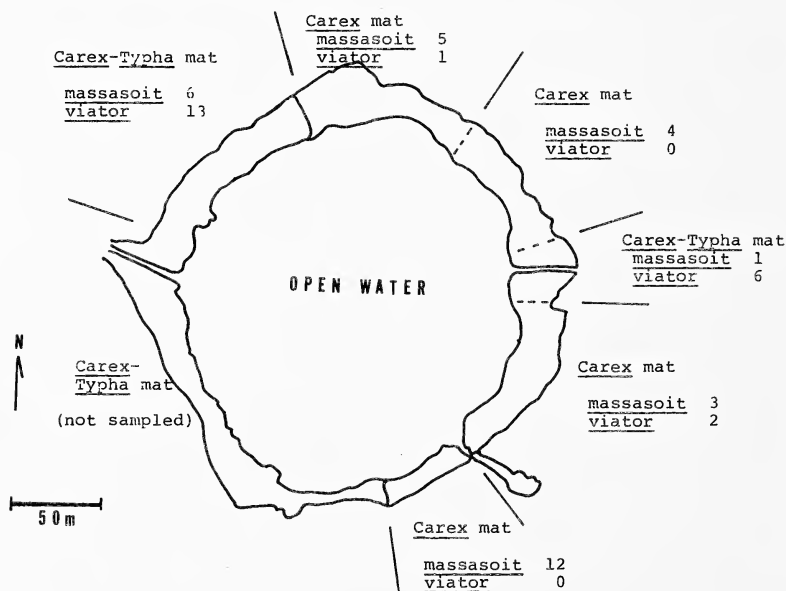
Fig. 2. The distribution of *Poanes massasoit* and *P. viator* at Mud Lake relative to the *Carex* and *Carex-Typha* mats. (Modified from Brodberg, 1976).

Once the habitat associations of each butterfly are known, patchy distributions are better understood and tend to reflect the distribution of certain habitat types. For example, only two wetland species, *Euphydryas phaeton* (Drury) and *Hyllolycaena hyllus* (Cramer), occur south of the glacial maxima where only swamps and poorly developed sedge meadows occur. More subtly, the known distribution of *P. massasoit* in Ohio coincides with the distribution of fens in the western part of the state. Additional sampling will probably locate this species in more of the western Ohio fen areas. However, not all aspects of wetland butterfly distributions are satisfactorally explained by the distribution of differing habitat types. *P. massasoit* is not present in the eastern part of the study area despite the presence of seemingly suitable habitats there.

Four other butterflies are present only in the western study sites, possibly the result of their past biogeographic histories. *E. dukesi* and *C. muticum* are both distributed along the Mississippi Valley (Opler, 1984) and may have migrated from this area into the Great Lakes Region via the valley and its tributaries after the last glaciation. *O. poweshiek* and *Epidemia dorcas* (Kirby) are distributed to the west of the study area and may have migrated eastward along the glacial front as habitats became available from their refugia. Thus, the absence of these species from certain regions may indicate the lack of suitable habitats during the periods of range expansion.

Several related pairs of ecologically segregated species occur in wetlands. These species pairs are usually more closely related to each other than to any other species in the study area. The evidence indicates partitioning of larval resources within the pairs but not with other species or between the species pairs. Shapiro and Carde (1970) reported that *S. eurydice* and *Satyrodes appalachia* (Chermock) segregate on the basis of open versus wooded habitats, a finding supported by this study. Although at certain localities where both species occur, they may utilize the same hostplant species which is effectively partitioned between them. *Eurydice* uses the hostplant in sunny areas and *appalachia* uses the hostplant in shaded areas.

Three other pairs of wetland butterflies also show similar segregation.

Euphyes dion (Edwards) — *E. dukesi*. These species segregate much as do *eurydice* and *appalachia*. Both species are usually associated with *Carex lacustris*, but *dion* occurs in open areas while *dukesi* occurs in shaded habitats. Only once have I observed *dion* inside a swamp feeding on buttonbush. At Marsh Lake, males of both species have been observed feeding in a hay field which ajoins the wetland complex, but within the wetland itself these species do not mix. Of the remaining wetland *Euphyes spp.* in the study area *Euphyes conspicua* (Edwards) is capable of utilizing several *Carex spp.* in open situations, while the hostplant and habitat associations of *E. bimacula* are not well known.

Poanes viator — *P. massasoit*. Although populations of these species often coexist in sedge meadows, they usually occur in close association with their respective presumed hostplants, *Carex stricta* Lamborn and *C. lacustris*. Both hostplants often form dense stands which superficially resemble monocultures with which the butterflies are intimately associated. I surveyed Mud Lake to identify the principal areas of activity for these two species. In this fen *Carex aquatilis* Wahlenb., a narrow leaved species, dominates the *Carex* mat and occurs less frequently in the *Carex-Typha* mat. *Massasoit* occurs throughout the fen but was most frequently found on the *Carex* mat while *viator* is more restricted and occurs on the *Carex-Typha* mat (Figure 2). At Marsh Lake, where both hostplants form monoculture like stands, the separation of these species is virtually complete although they are often seen at the same nectar sources.

Epidemia dorcas — *E. epixanthe* (Boisduval and Le Conte). These species segregate by both hostplant and by habitat. *E. epixanthe* was not encountered during this study: its hostplant, large cranberry (*Vaccinium macrocarpon* Ait.), is restricted to highly acidic peat deposits and only forms dense stands in bogs. In fens, *V. macrocarpon* often occurs in older more acidic parts of the mat or in sphagnum hummocks at the base of shrubs, but only as dispersed plants and never in dense stands. *L. dorcas* utilizes shrubby cinquefoil which is limited to alkaline peat deposits (i.e. fens). Thus, populations of these two butterflies would not be expected to interact at any given locale.

How these species pairs formed within the wetlands of eastern North America is an interesting question. Because ecological disassociations found in this study are uniformly restricted to closely related species, the disassociations may represent ecological isolating mechanisms. This appears to be the case in the examples cited of wetland *Satyrodes, Euphyes,* and *Poanes*, which showed no evidence of interspecific courting/mating during this study. Other factors may have helped shape these species pairs. Although no direct evidence exists to support such conjecture, it is interesting to speculate that some process such as interspecific competition for hostplants (Shapiro & Carde, 1970) or divergence of isolated populations within the limited confines of a few wetlands has resulted in the formation of such species pairs. (See Shapiro, 1970). Genetic exchange between many of the populations in this study must be minimal to non-existent due to the vast expanses of unsuitable habitat separating them, but it is unknown how freely populations mixed before humankind altered the landscape or during the previous interglacials. It must be assumed that all of these species possess some dispersal capabilities or they would not occur within glaciated territory.

No doubt the repeated destruction and reformation of wetland habitats during glacial cycles has had a profound effect upon these communities.

Each advance of the ice sheet presumably fragmented and relocated populations of each of these butterflies, possibly to small refugia where certain populations may have been more susceptible to environmentally induced genetic changes. Additionally, each wetland itself slowly undergoes natural succession. These changes (e.g. fens becoming acidic or marshes, fens and bogs becoming wooded) may be gradual enough to allow the subtle ecological differences observed between some of the closely related species to evolve.

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Notes on *Gnathmocerodes petrifraga* **Diakonoff 1967** (Lepidoptera: Tortricidae) associated with *Barringtonia* **Trees**

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Abstract. *Gnathmocerodes petrifraga* Diakonoff, 1967 (Lepidoptera: Tortricidae) is recorded for the first time from the Indochinese Peninsula (southeastern Vietnam). The larvae feed on leaves of *Barringtonia acutangula* L. (Lecythidaceae) growing in inundated semiaquatic habitats of lowland rivers. No seasonal occurrence of *G. petrifraga* was observed and its larvae were found in dry and wet seasons. A short taxonomical diagnosis is presented with a new description and illustration of the female genitalia. The species is closely related to *G. lecythocera* (Meyr.).

Introduction

The genus *Gnathmocerodes* s.str. Diakonoff, 1967 (Tortricidae: Olethreutini) is represented by three species in the Oriental Region. There is a great probability that all the species are associated with *Barringtonia* trees (Lecythidaceae), but few data are available (Diakonoff, 1967, 1973). Our paper presents field ecological investigations of *G. petrifraga* Diakonoff, 1967, in southeastern Vietnam, with notes on its taxonomy.

Material Examined

The investigated larvae of *G. petrifraga* were collected on trees of *Barringtonia acutangula* L. growing in the lowland river Song Kinh Dinh near Nha-Ho, 11°37'58"N, 108°52'19"E, 15 km West of Phan Rang, S.E. Vietnam, in April 1982 (dry season) and October 1984 (wet season). The environment of the Phan Rang Plain near Nha-Ho is treated briefly by Spitzer (1983). The larvae were reared under tropical laboratory conditions and six adults (4 males, 2 females) were obtained: 20 April 1982 — 2 males, 1-7 November 1984 — 2 males, 2 females.

Taxonomic Diagnosis

G. petrifraga was described by Diakonoff (1967), including morphological characteristics of male genitalia. Only two males (holotype and paratype) were recorded from the Philippine Islands (Luzon) and India (Calcutta). A supplementary characteristic feature is the shape of the medial process of the valva terminally covered with obtuse spines (Fig. 1). The same shape of the process, with a long stem, is developed on both valvae, one of which is not visible in Diakonoff's (1967) original holotype illustration. The female genitalia were not described and their general appearance is very similar to those of *G. lecythocera* (Meyr.) (not *G. tonsoria* Meyr. - see Diakonoff, 1973): Sterigma with posterior edge slightly curved, signum bursae long, narrow and pointed with a large basal plate (Figs. 2, 3).
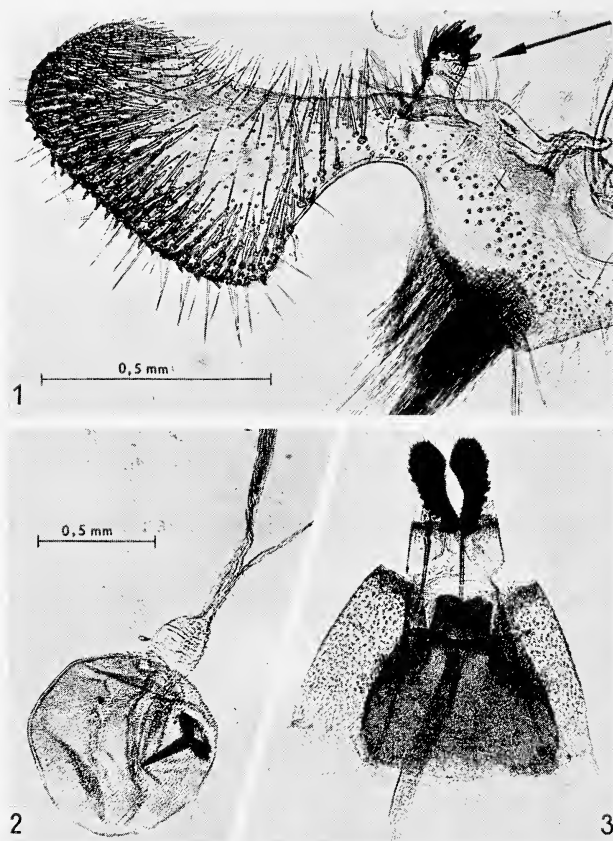
Figs. 1-3. *G. petrifraga* Diakonoff: Fig. 1. male genitalia (valva with process indicated by arrow), Figs. 2-3. female genitalia.

Field Observations and Discussion

The larvae of *Gnathmocerodes petrifraga* Diakonoff were found feeding in rolled or folded leaves of *Barringtonia acutangula* L. growing in a large lowland river Song Kinh Dinh of the Phan Rang Plain (monsoon seasonal "savanna" region - see Spitzer, 1983) (Fig. 4). *Barringtonia acutangula* is a typical small tree of the inundated vegetation of Indochinese freshwater formations (Vidal, 1979). The other characteristic plants of Song Kinh Dinh are shrubs of *Homonoia riparia* Lour. (Euphorbiaceae) and *Combretum quadrangulaqre* Kurz. (Combretaceae). During the wet season (October) the water level of the river rises as much as 5 m and only some crowns of *Barringtonia* trees stick out above the water surface.

G. petrifraga was found to be probably an obligatory species associated closely with *Barringtonia acutangula* during both the wet and the dry season in Vietnam. *Barringtonia* trees are the only known food plants of *Gnathmocerodes* (s.str.) species. An exception is *G. lecythocera* (Meyr.) from Java feeding on other two plants (see Diakonoff, 1973). The larvae pupated in light silk cocoons in spun leaves and the pupae (n=6) developed with 7-11 days (t=26-32°C). The larvae and pupae are probably highly adapted to the changing water level of the inundated *Barringtonia* ecosystem. The other few lepidopterous species that we found feeding on *Barringtonia acutangula* in Vietnam are polyphagous and widely distributed: *Theretra nessus* (Drury) (Sphingidae) and *Cabanilla* sp. (Lymantriidae). Some ecologically opportunistic species of *Theretra* and *Trabala* (Lasiocampidae) have been recorded by Barlow (1982) feeding on *Barringtonia* sp. in Malaya. Thus *Gnathmocerodes petrifraga* Diakonoff is the only well-adapted stenotopic and nonseasonal species of Lepidoptera, which is characteristic of the inundated *Barringtonia* vegetation type.

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Fig. 4. Habitat of *G. petrifraga* Diakonoff: *Barringtonia acutangula* trees in Song Kinh Dinh, S.E. Vietnam.

The Impact of Pierid Feeding on Seed Production by a Native California Crucifer

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Abstract. Feeding by an inflorescence/infructescence-consuming Pierid, probably *Anthocharis sara stella*, destroyed between 41 and 49% of potential seed output in an isolated stand of the native Sierran Crucifer *Arabis holboellii* var. *pinetorum*. Damage was concentrated on leaders, probably for phenological reasons.

Ever since Hairston, Smith, and Slobodkin (1960) argued that herbivores could not be food-limited because "the world is green," ecologists have labored to understand whether and why this should be the case. Several quantitative studies have now appeared on patterns of utilization of Cruciferous hosts by Pierid butterflies. These have revealed complex situations in which both direct and indirect evidence for both intra- and interspecific competition has been adduced. The present paper reports an instance of very intense damage to the developing fruits (siliques) of a native Sierra Nevada Crucifer, *Arabis holboellii* Hornem. var. *pinetorum* (Tides.) Roll. The case is of special interest because the entire plant population could be censused and the pattern of damage determined with considerable precision.

The plants were located in dry Jeffrey Pine—Incense Cedar—White Fir forest with *Ceanothus* and *Ribes* understory, along the California-Nevada border about 3 km N Verdi, NV (2000 m). They formed a discrete population, with no conspecifics observed in any direction for a distance of 0.75 km. The only other Crucifers found within this circle were four *Lepidium virginicum* var. *pubescens* (Greene) Thell. and several vegetative rosettes of *Rorippa* sp. in a seep. All were undamaged. All *Arabis* were examined on 6 July 1984 and the following data collected: height, phenophase (vegetative, flowering, fruiting), number of intact and missing or damaged siliques per branch. Rarely, damage to the apical portion of the shoot was so severe that the number of missing siliques had to be estimated. Damage estimates are systematically low, because no attempt was made to assess potential reproduction lost by destruction of flowers or buds. The term "leader" used in this paper refers to the central axis which develops first from the rosette. "Branch" refers to products of axillary buds on this axis, which do not bloom until after the "leader" to which

they are attached has done so. Two plants were missing the distal portions of their leaders due to vertebrate (probably rabbit) grazing. The complete results are reported in Table 1.

If all siliques are treated as equal, total loss of reproductive potential in the population was 41%. For the 13 plants which suffered damage, this increases to 49.1%. Two plants—one the largest in the stand—suffered no losses. Damage was much less severe on side branches. On plants sustaining damage, the ratio of intact to damaged or lost siliques was 43:116 for leaders, 78:1 for branches. Branches were almost inevitably much shorter than leaders and were produced later. Some branching may be in response to damage, but undamaged plants also branch. Several

Table 1.   Census of *Arabis* plants at a forest site near Verdi, NV, 6 July 1984.

Height of leader (cm)	Number of intact siliques, by branch	Number of damaged or missing siliques, by branch	Height of leader (cm)	Number of intact siliques, by branch	Number of damaged or missing siliques, by branch
76	22	0	35.5	6	4
	3	0		2	0
	4	0		3	0
	3	0	20.3	0	13
	5	0		3+	0
51	7	8		1	0
	5+[1]	0	23	3	12
	2+	0	(two leaders)		
30.5	1+	9		3	0
25	(tallest branch) —— leader missing[2]		2	0	
	1	0		6	0
	2	1		0	10
60	0	8		2	0
	11	0		2	0
	16	0		3	0
23	(tallest branch) —— leader missing[2]	50	16	2	
	4	0	36	0	14
	5	0		4+	0
25	1	16	21	6	0
38	1	12	35	2	8
	3	0			
	3	0	Vegetative rosettes: 35 plants.		
	4	0	**Total Siliques:**	**167**	**117**

[1]+indicates still in flower.
[2]rabbit damage.

branches were still in flower, but no leaders were. Presumably the difference in damage to leaders vs. branches reflects phenophase when the females were ovipositing—not a "preference" for one or the other.

Although no larvae were found at the site, frass was present and the only infructescence-feeding Pierid common in the area is *Anthocharis sara stella* W. H. Edwards. This is a red-egg species (Shapiro, 1981a) which normally lays only one egg per inflorescence, and the larvae cannibalize both eggs and smaller larvae (Shapiro, unpubl.), so that it is very rare to find more than one larva on a leader though there may be several on a large, bushy, multi-stemmed plant. The difference in damage to leaders vs. branches would only be apparent if the leaders were themselves sufficient to support the full development of the larva. This seems to be the case, since nearly all leaders had a significant number of "left-over," undamaged siliques and the amount of damage was sufficient, based on rearing experience, to carry the larvae through to pupation.

One plant had twin basal rosettes, each with its own leader. The intact: damaged or lost ratios for the siliques were 3:12 and 0:10 for the leaders and 11:0 and 7:0 for their respective branches.

No information is available on seed quality or germinability from leaders vs. branches. Siliques are almost invariably smaller on branches than in corresponding positions on leaders.

Discussion

Virtually all Pierid-Crucifer studies find a conspicuous "edge effect," that is, the impact of the herbivore is disproportionately high on isolated and marginal individuals of the plant and low deep within stands. This is true on weedy Crucifers (Shapiro, 1975, 1981a,b, 1985a) but also on native species (Shapiro, 1981b,c). Any situation in which there is high intrapopulation variance in either survivorship or reproduction is potentially a case of natural selection at work. The "edge effect" results in such a variance, but unless central and peripheral plants differ in a heritable way (such as seed size, translating into dispersability), selection is unlikely to follow. If site (central vs. peripheral) is determined probabilistically, and the consequences of drawing a bad site are catastrophic, the selective result should be the acquisition of anti-herbivory mechanisms by the population as a whole (such as the "false eggs" of some *Streptanthus*, Shapiro, 1981a,c). However, most Pierids are phenological specialists; many require plants in bud or early flower for oviposition. The distribution of damage may then be due to the degree to which the butterflies and plants are "in phase." If damage is strongly correlated with phenology (Shapiro, 1985b), herbivory may select for earlier or later blooming (if the insect emergence time is predictable, and "all else being equal"), or for a "risk-spreading strategy" with high intrapopulational variance in phenology (if the insect is unpredictable).

In this stand of *Arabis*, the evidence suggests that oviposition was concentrated in a short period of time. In a compact stand contained within 1.5 ha in an open environment easy to search, 86.6% of the plants in the appropriate phenophase were damaged. Subsequent branching may allow at least the larger and more vigorous plants to recoup their losses. Only long-term phenological studies can reveal whether a directional shift in blooming time is to be expected as a result of herbivory.

The distribution of many native montane Crucifers appears superficially similar to the *Arabis* near Verdi: relatively local and isolated populations of moderate to occasionally high density. This may be the historically "normal" context in which ecological and evolutionary phenomena relating to host selection and competition have evolved in the Crucifer-Pierid system. Heavy but spotty damage, strongly affected by the phenology of both butterfly and plant (and thus by weather), may be much more "normal" than the very low levels of damage commonly observed in weedy systems. The searching behavior of females, egg-load assessment, cannibalism and convergence may all be much more explicable under these circumstances than in the more familiar, highly disturbed ones where they are usually studied.

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Notes

An Intersubfamilial Courtship (Lycaenidae)

Reports of interspecific courtship are of interest because they help to define the stimuli whereby species- and sex-recognition take place. They are relatively rare in Lepidoptera (cf. Stamps and Gon, 1984, Ann. Rev. Ecol. Syst. 14:231-252), but the actual phenomenon is not: interspecific courtships are encountered surprisingly frequently in field work with butterflies (cf. Shapiro, 1973, J. Lep. Soc. 27:159, J. Res. Lepid. 11:197-198; 1983, J. Res. Lepid. 20:54). The present report concerns a courtship involving two subfamilies of the Lycaenidae (Lycaeninae and Theclinae).

At 1332 h on May 19, 1984, at Lang Crossing of the South Yuba River, west slope Sierra Nevadas, Nevada Co., Calif., ca. 1660 m elevation, a male *Lycaena cupreus* W. H. Edwards was seen courting a female *Mitoura nelsoni* Bdv. which was nectaring at a flower of *Lepidium campestre* (L.) R.Br. (Cruciferae) about 15 cm above the ground. The female did not appear to notice the male at all. At 1334 he was joined by a second *L. cupreus* male, and the two then alternated positions sitting adjacent to or behind the female and flying about her during the following two and-a-half minutes. At about 1337 the second male flew off; the first male continued courtship another minute, at the end of which the female, which had moved only far enough to shift her proboscis from one flower to the adjacent one, suddenly flew. The male did not follow. The interaction thus lasted at least 6 min.

Weather conditions were: clear, light SW wind, low humidity, air temperature ca. 25°C. Both species were common in the area and fresh. The sex-ratio of *M. nelsoni* at flowers was seemingly close to unity, but only one female of *L. cupreus* was seen all day as against at least 20 males. No sexual activity was seen in *M. nelsoni*. In the morning *L. cupreus* males were mostly perching on bare soil and pursuing passing insects, but in early afternoon this activity had nearly ceased and most males were at flowers of *L. campestre*, the only common nectar source in the area. Not having seen the initiation of the courtship I cannot comment on the nature of the attractive stimulus, but the second male *Lycaena*, which had been passing by, was obviously attracted by the activity of the first male.

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A Bilateral Gynandromorph *Celastrina ebenina* (Lycaenidae)

A bilateral gynandromorph of the Dusky Blue (*Celastrina ebenina* Clench) was collected on 1 May 1984, near The Plains, Athens County, Ohio. At this locale, *ebenina* occurs abundantly on an abandoned railroad track along the north facing slope of the Hocking River channel. The host plant, *Aruncus dioicus* (Walt.), has apparently spread from an adjacent woodland and is common on the abandoned cinder bank.

Dorsally the left half of the specimen is male in appearance and is dark gray with a very light scattering of blue scales basally on both wings (Figure 1). The right half of the gynandromorph is female in appearance and both wings are gray along the costal area and distal margins. The median area of both wings are whitish-blue.

Ventrally there are several differences between the two halves especially in the configuration of several bands of spots, the most noticeable of which is the post median series of the forewing. In the male the individual spots that make up this series tend to angle sharply toward the wing margin, especially in cells mu_2-m_3 and m_3-cu_1. In the female half the individual spots run more parallel with the wing margin. Examination of additional specimens in the authors' collections indicate that this sexual difference is probably consistent.

The genitalia of the gynandromorph were dissected and determined to be male. Further, the genitalia show no abnormalities and easily fall within the range of variation seen in other Ohio material. The only prothoracic leg present (right) has fused tarsi, a male characteristic. The remaining legs, antennae and palps were examined, but no differences between the two halves of the gynandromorph were apparent. The gynandromorph is in the J. W. Peacock collection.
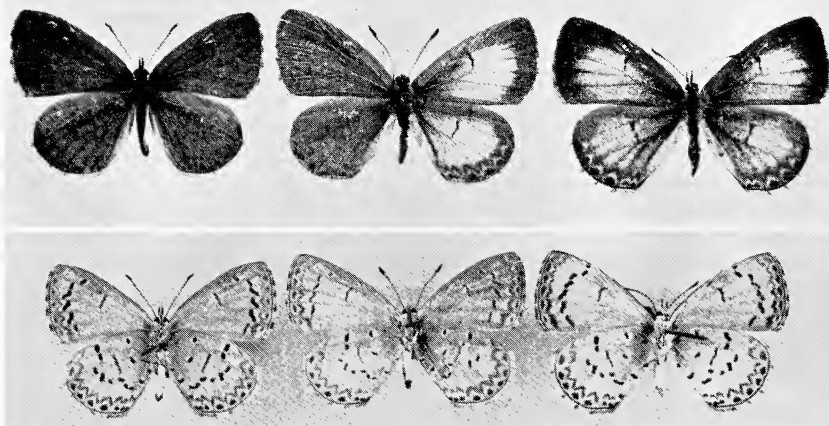
Fig. 1. Normal and gynandromorphic *Celastrina ebenina* from Ohio. Dorsal view (top row, left to right): Male, gynandromorph (left half male, right half female), and female. Ventral surface (bottom row, left to right): Male, gynandromorph (left half female, right half male), and female.

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ON THE LEPIDOPTERA

IN THIS ISSUE

COVER ILLUSTRATION: Series of photographs showing eclosion of *Caligo atreus*. See Young and Muyshondt, page 154.

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Opinion

A Rebuttal to the Arnold Classification of *Speyeria callippe* (Nymphalidae) and Defense of the Subspecies Concept

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Abstract. In a provocative paper (Pan-Pacific Entomologist 61:1-23), Richard A. Arnold has proposed that the taxonomic classification of subspecies within *Speyeria callippe* (Boisduval) should be essentially eliminated for three different reasons. These include (1) most subspecies are heterogeneous with much clinal intergradation, (2) most independent characters vary discordantly, and (3) most diagnostic characters are only "minor" or "slight" differences in wing color pattern. If these views are applied to the entire genus, the taxonomic classification of *Speyeria* below the species level would be nearly abolished. The present paper reviews and rebuts the methodology and conclusions presented in the Arnold study. The general philosophy of the subspecies concept is discussed with respect to *Speyeria*. It is argued that the differences between *Speyeria* subspecies are often far greater than between full species, and that the three criticisms of the subspecies concept presented by Arnold equally apply to most full species of *Speyeria*. Finally, it is also argued that *Speyeria* subspecies represent tangible and significant units of evolutionary divergence, and that the historical classification of *Speyeria* subspecies is fully warranted and should be retained.

The nymphalid butterfly genus *Speyeria* is well known for the tremendous diversity of geographic variation in wing phenotype evident throughout most of the group. This variation was once recognized by the taxonomic classification of over 100 typological "species" within the genus. Later, dos Passos and Grey (1947) found evidence of extensive clinal intergradation among many of these "species", therefore reducing these taxa to subspecies status. As a result of their study, the diversity observed within *Speyeria* was reclassified into 13 biological species.

Recently, Arnold (1985) has conducted a complex statistical study of the geographic variation found in one of these species groups, *Speyeria callippe* (Boisduval). On the basis of this work, Arnold concluded that most of the geographic variation perceived within *S. callippe* is not statistically significant, and that the taxonomic classification of subspecies should be essentially abolished. Moreover, the geographic variation seen

in *S. callippe* is quite typical of the genus as a whole. If this approach and philosophy were applied to the entire genus, the taxonomic classification of *Speyeria* below the species level would be virtually eliminated.

However, Arnold's study is subject to vigorous challenge regarding the accuracy and validity of both its methodology and data. In addition, the more basic philosophy expressed in this paper regarding the subspecies concept and taxonomic classification is also subject to strong debate. Both of these issues will be addressed in this review of the Arnold study.

Many errors and deficiencies are evident in the data and methodology employed by Arnold in his study. He has used the statistical techniques of variance analysis, principal components analysis, and discriminant function analysis to examine geographic patterns in eight different wing characters. The first error lies in his choice of characters used for analysis, which include five wing dimension characters and three color pattern characters. Contrary to Arnold's statement on page 4 of his paper, wing size has never been regarded as a particularly significant component of the geographic variation within *Speyeria callippe* or in the taxonomic delineation of subspecies. Wing length is only of significance when comparing geographically contiguous populations or subspecies, for example San Francisco *S. c. callippe* and inland *S. c. comstocki*. Characters of wing pattern and color are the primary factors involved in the geographic variation of this species as outlined in an earlier paper (Arnold, 1983). As a consequence, five of the eight characters used by Arnold in his analysis are essentially irrelevant to the larger patterns of geographic variation within *S. callippe* and should have been excluded from the study.

Thus, only three characters of wing color pattern that do exhibit significant geographic variation, were used in the study including dorsal ground color, ventral disc color, and ventral spot silvering. However, there are serious flaws in Arnold's analysis of these characters as well. Moreover, it appears that Arnold has substantial errors in his taxonomic concepts of *S. callippe* subspecies as shown in his page 2 map. These errors are outlined as follows:

1. Arnold placed *S. c. meadii* in northwestern Colorado. However, this subspecies is limited to the Colorado Front Ranges east of the Continental Divide. Populations in western Colorado are closer to subspecies *S. c. harmonia*.

2. Arnold placed *S. c. nevadensis* across Nevada, but placed *S. c. laura* east of Lake Tahoe. In fact, the subspecies *S. c. nevadensis* is limited to the Sierra Nevada east slope in eastern California and western Nevada. Populations in central and eastern Nevada belong to subspecies *S. c. harmonia*. The name *"laura"* is not known to represent any discrete population, but was applied to an extreme individual in Sierran *S. c. nevadensis* populations near Lake Tahoe.

3. Arnold largely ignored the important geographic variation in *S. callippe* across the Sierra Nevada, perhaps because of the considerable taxonomic confusion that currently surrounds this variation. The unsilvered populations at low elevations along the west slope of the Sierra Nevada are properly called *S. c. inornata* rather than *S. c. juba* as denoted by Arnold. Both taxa were originally described from Downieville, Sierra County, although this type locality is not particularly appropriate for either taxon. Relatively uniform or "pure" populations of *S. c. inornata* are actually restricted to the low foothills extending from northern Tulare County north to Shasta County. Although the name *"inornata"* may pose a nomenclatural problem, these populations comprise a very distinctive subspecies that certainly warrants recognition.

4. The names *juba* and *sierra* apply to silvered populations at high elevations that intergrade between *S. c. inornata* and *S. c. nevadensis* along a sharp east-west stepcline. Populations found on the west slope (i.e. Quincy-Downieville region) resemble the lectotype of *S. c. laura*, but the designated type locality of *laura* at Carson City, Nevada, is not appropriate. The populations on the east slope (i.e. Mt. Ingalls-Gold Lake region) have been named *S. c. sierra* dos Passos and Grey. However, L. Paul Grey (pers. comm.) has recently examined the lectotype of *S. c. juba*, and found that it matches the phenotype of the east slope subspecies. Thus, the name *sierra* must be regarded as a synonym of *S. c. juba*, and the actual type locality is probably closer to Gold Lake rather than Downieville.

5. Arnold has transposed the names *laurina* and *macaria* on his page 2 map, since *S. c. macaria* occupies the Tehachapi Mountains while *S. c. laurina* occurs on the west slope of the Greenhorn Mountains. Presumably the samples shown in his Table 1 are correctly identified.

Detailed descriptions of the *S. callippe* subspecies together with their distributions are outlined in Appendix I.

A third major flaw in Arnold's analysis is the failure of his methodology in detecting significant geographic variation in dorsal wing color as outlined by Hovanitz (1943). A particularly dramatic example of this is the comparison of the San Francisco *S. callippe callippe* with *S. c. liliana* of Napa and Lake Counties. The typical *S. c. callippe* subspecies is one of the most divergent and distinctive taxa within the species. It is characterized by pale yellow-orange ground color combined with extremely intense melanic suffusion on the dorsal wing surfaces. In addition, the subspecies exhibits a dark to medium brown disc covered with extensive yellow overscaling on the ventral hindwing. By sharp contrast, *S. c. liliana* exhibits a darker reddish orange ground color on the dorsal surfaces combined with reduced melanic basal suffusion. Furthermore, *S. c. liliana* exhibits a solid, dark red-brown disc with little or no evidence of yellow overscaling. I have examined several hundred specimens of both *S.*

c. callippe and *S. c. liliana*, and these differences are nearly constant at a frequency greater than 90%. Yet Arnold completely fails to resolve this extreme divergence in his own analysis outlined in his Figure 7. The only *S. callippe* subspecies that even remotely resembles the typical subspecies are the *S. c. comstocki* populations of the central-southern Coast Range, and these are consistently paler in color with reduced melanic suffusion compared to the San Francisco populations (see below). It is not clear why Arnold's methodology has failed in the analysis of dorsal coloration, but perception problems in the scoring of the raw data are a possibility.

A fourth error is seen in the analysis of spot silvering on the ventral hindwing, which may be due to faulty data. The unsilvered form is largely restricted to low elevations along the west slope of the Sierra Nevada and in the Salmon-Siskiyou Mountains of northern California. This trait is very rare or completely absent in populations along the east slope of the Sierra Nevada. Yet Arnold depicts a very high frequency of unsilvering east of Lake Tahoe in his Figure 8, which is certainly not seen in the *S. callippe nevadensis* populations of that region. I would suspect that his sample of *S. c. "laura"* specimens may have faulty locality data.

A fifth error is seen in the analysis of ventral disc color, which undoubtedly reflects inadequate sampling and geographic coverage. In his Figure 9, Arnold suggests that there is a sharp geographic discontinuity between the green and brown disc forms with very little overlap in populations. This is simply not true. In fact, the green form dominates in populations along the east slope of the Sierra Nevada from Inyo County north to Lassen County, and there is extensive mixing of the green and brown forms together with intermediates in populations extending from Eldorado County north to Klamath County, Oregon. Moreover, the *S. c. semivirida* populations are also extremely heterogeneous in disc color, with green, brown, and intermediate color forms occurring together throughout the populations extending from southern Oregon to British Columbia and east to western Idaho. Therefore, since extensive mixing of disc colors does in fact occur within populations over wide geographical areas, disc color can not be used as a single diagnostic character to distinguish subspecies. Hence in accordance with Arnold's philosophy, virtually no taxonomic subspecies within *S. callippe* should be recognized!

However, this philosophy concerning the subspecies concept and its taxonomy requires close scrutiny. The questions raised by Arnold in his treatment of *Speyeria callippe* received a long and extensive debate several decades ago, and Pimentel (1959) has provided a good review of this debate. Certainly these questions have direct relevance to the taxonomic classification of *Speyeria*.

Geographic subspecies exhibit the following characteristics when

strong isolating barriers are either presently absent or were absent in the relatively recent past (i.e. 15,000 years ago):

1. Subspecies exhibit clinal intergradation with other subspecies in geographically contiguous regions.

2. Subspecies rarely exhibit complete homogeneity for any single character, and most characters are shared by more than one subspecies.

3. Independent characters usually exhibit discordant geographic variation.

4. As a consequence of the above, most subspecies are defined by a particular combination of characters which occur at a reasonably high frequency within the populations of the subspecies.

The absence of these features when no geographic barriers are present suggests reproductive isolation and full species status. Therefore, these characteristics serve to distinguish the subspecies from the fully distinct species.

As an example of this phenomenon, *S. callippe macaria* and *S. c. laurina* share pale dorsal ground color, reduced basal suffusion, a pale brown to yellow disc, and a wide submarginal band on the ventral hindwing. The two subspecies differ in that *S. c. macaria* populations usually have silver spots at a frequency of 90% or more, while *S. c. laurina* populations have unsilvered spots at a frequency of 60% or more. Sette (1962) has outlined the gradual clines between these populations in the frequencies of this silvering character. Likewise, the subspecies *S. c. elaine* (silvered) differs from the subspecies *S. c. rupestris* (unsilvered) in exactly the same way. However, the *elaine-rupestris* subspecies differ from the *macaria-laurina* subspecies by combining the silvering characters with extremely dark ground color, melanic basal suffusion, a dark brown disc, and a narrow submarginal band.

It is generally agreed that populations along gradual clines should not be recognized as discrete subspecies, but populations at points along a sharp stepcline may warrant recognition. As an example, one may arbitrarily define populations as *S. c. macaria* if the frequency of silver spots is 60% or more, or as *S. c. laurina* if unsilvered in similar frequencies. Thus, populations in the Tehachapi Mountains may be called *S. c. macaria*, populations on the west slope of the Greenhorn Mountains may be called *S. c. laurina*, and populations in the Piute Mountains may be called *S. c. macaria-laurina* intergrades.

Because most independent characters vary discordantly and along gradual clines, and because most populations are not homogeneous as a result, Arnold and many others have argued that subspecies are merely arbitrary categories that have no real meaning or significance. Instead, these authors suggest that the proper way to look at geographic variation is to examine the distribution patterns of single genes or character state

frequencies, and attempt to correlate these patterns with environmental variables. While this approach is certainly of value, it does not substitute for the subspecies concept. Individual genes or character states do not exist completely detached in time and space, but belong to populations which occupy discrete geographic distributions. Moreover, it is the population that adapts to a particular set of local environmental conditions, and is the basic evolutionary unit as discussed by Ehrlich and Murphy (1981) for *Euphydryas*. Individual genes or characters are certainly not evolutionary units. In addition, geographic subspecies are the immediate precursors of full species, and are of prime importance to the basic process of allopatric speciation. The fact that most subspecies are not clearly homogeneous or sharply delimited does not alter their evolutionary importance.

With regard to the taxonomic nomenclature of subspecies, many objections have been raised to the Latin trinomen, and Arnold suggests that this classification should be largely abolished because trinominal systems "distort the real nature of character variation and bias subsequent analysis". However, it is not sufficient to consider individual genes or characters as mere abstractions completely isolated from actual populations. It is necessary to recognize populations as evolutionary units distributed in time and space, and some type of nomenclature is also necessary to recognize and discuss those populations that exhibit significant evolutionary divergence. Wilson and Brown (1953) agree with this to some extent, but suggest that the trinominal names of subspecies should be discarded in favor of vernacular names such as the "Pine Mountain Silverspot" or the "Grass Valley Silverspot". Of course the problems of ambiguity and confusion with vernacular names when applied to scientific nomenclature are well known (see Murphy & Ehrlich, 1983; Pyle, 1984). In addition, the trinominal system has a long, historical establishment in the literature, and is widely familiar to most students of the various taxonomic groups. To completely replace an established classification with an entirely new system would be extremely confusing, and is entirely unwarranted.

Perhaps the most serious concern with Arnold's classification of *Speyeria callippe* is his perception of "significant difference". He frequently refers in his paper to the differences between subspecies as "slight", "minor", and "minute". In his discriminant analysis, he was only able to correctly identify 43.2% of individuals of unknown subspecific identity. Of course, part of this problem is due to the heterogeneous overlap between subspecies along clines. However, fundamental problems in the perception of actual character differences are evident in his study. The characters used to distinguish subspecies are the same characters used to distinguish fully distinct species of *Speyeria*. Indeed, the differences in wing color pattern between subspecies are often

far greater than between full species throughout their ranges!

For example, *S. callippe callippe* differs from *S. callippe inornata* by five different characters of wing color pattern. In sharp contrast, sympatric *S. atlantis dodgei* (Gunder) and *S. hydaspe* (Bdv.) only differ consistently by one color character, and even this character often requires close examination by the human observer for correct identification. There are dozens of similar examples where the differences between subspecies are far greater than between full species. Indeed, only three species of *Speyeria* exhibit constantly diagnostic wing pattern characters, namely *S. diana* (Cramer), *S. idalia* (Drury), and *S. nokomis* (Edwards). None of the other species have completely exclusive, diagnostic wing characters that do not overlap with other species in parts of their respective ranges. Thus, *S. zerene bremnerii* (Edwards) of the Pacific Northwest is extremely similar to *S. atlantis nikias* (Ehrmann) of the southern Rocky Mountains, and many specimens can only be distinguished on the basis of geography alone. Yet sympatric populations of *S. atlantis* and *S. zerene* are usually highly divergent and easily identified. If Arnold can not distinguish *Speyeria* subspecies because the differences are too "slight" or "minor", he will have exactly the same problems distinguishing between full species.

It is useful to look at Arnold's perception problems in more detail by re-examining several of the populations used in his study. As previously discussed, the typical San Francisco *S. callippe callippe* is one of the most divergent subspecies seen within the entire species. The only similar subspecies is the more inland and southerly *S. c. comstocki*. Arnold has concluded that these subspecies can not be distinguished. While they are certainly heterogeneous with some degree of overlap in characters, these subspecies exhibit significant divergence in three color pattern characters, and they also differ significantly in average forewing length as well.

First, typical *S. c. callippe* has extremely intense melanic suffusion on the dorsal wing surfaces, while the suffusion is more reduced in *S. c. comstocki*. The suffusion in *S. c. callippe* extends to the distal parts of the wings, combined with heavy dark scaling that extends out along the veins. As a consequence, the pale dorsal median areas that correspond to the silver median spots on the ventral hindwing contrast sharply with the distal ground color. Most specimens of *S. c. comstocki* do not exhibit this sharp contrast.

The second character is the yellow overscaling on the brown disc of the ventral hindwing. Many specimens of *S. c. callippe* retain solid brown areas on the disc that are free of this yellow suffusion, particularly in the costal and limbal areas of the disc. Most specimens of *S. c. comstocki* exhibit yellow suffusion over nearly the entire disc.

The third character is the reddish ground color that covers the basal

region of the ventral forewing. In males of *S. c. callippe*, this red color extends beyond the discal cell out into cells Cu 1 and Cu 2 almost to the black median bars or even beyond. In the males of *S. c. comstocki*, this red color is largely restricted to the discal cell itself.

For the above analysis, 45 males of *S. c. callippe* from San Bruno Mountain in San Mateo County were compared with 52 males of *S. c. comstocki* from three sites in the Diablo Range. These localities are 20 miles south of Livermore in Alameda County, near Milpitas in Santa Clara County, and Del Puerto Canyon in Stanislaus County. The results are shown in Table 1. Although some degree of overlap exists between *S. c. callippe* and *S. c. comstocki* for all characters studied, this overlap is very minimal with respect to the dorsal melanic suffusion and the ventral red coloration of the male forewing. Regarding the disc colors, the frequency of light and dark color is about equal in the *S. c. callippe* sample, but the frequency of dark color is significantly reduced in the *S. c. comstocki* sample (X^2 p<.0001). The range of *S. c. comstocki* forewing lengths is 24-29 mm with the majority of specimens falling in the 26-27 mm classes. By contrast, the range of *S. c. callippe* forewing lengths is 28-32 mm with the majority of specimens falling in the 29-30 mm classes. While no single character trait is exclusively confined to either subspecies, the general pattern of character frequencies is one of very strong divergence between the *S. c. callippe* and *S. c. comstocki* subspecies.

Therefore, it is concluded that Arnold's study has failed to perceive the major differences that actually exist among the diverse subspecies of *Speyeria callippe*. Significant divergence between geographically contiguous subspecies such as typical *S. c. callippe* and *S. c. comstocki* is a tangible reality, despite some degree of heterogeneous overlap between such populations. More remotely spaced subspecies such as *S. c. comstocki* and *S. c. rupestris* exhibit a far greater degree of evolutionary divergence as one might expect. At the most extreme level of divergence, as between *S. c. rupestris* and *S. c. harmonia*, one would never suspect that such taxa belonged to the same species or were even remotely related. The conspecific relationships of such extremes are only known because of the existence of intergrading populations along gradual clines. Early authors had quite valid reasons to believe that such taxa were fully distinct species when they were first described. The subsequent discovery of intermediate clinal populations does not mean that this evolutionary diversity and adaptive radiation within *S. callippe* no longer exists or is not a reality. Divergent populations require recognition and some type of taxonomic nomenclature for discussion purposes. Merely describing the distribution frequencies of individual genes or character traits detached from actual populations is completely inadequate.

Subspecies represent significant levels of evolutionary divergence, often nearly as much as full species. The heterogeneous overlap between

contiguous subspecies or the discordant variation of independent character traits does not reduce this significance. Thus, it is suggested that the historical subspecies classification of *S. callippe* and other species of *Speyeria* should be retained, because such a classification serves to recognize important evolutionary phenomena.

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Table 1. Frequencies of dorsal melanic suffusion, ventral red color, and disc color in samples of *Speyeria callippe callippe* and *S. c. comstocki*.

	intense suffusion	light suffusion	intense red	reduced red	dark disc	light disc
callippe (n=45)	.93	.07	.93	.07	.49	.51
comstocki (n=52)	.10	.90	.15	.85	.15	.85

Appendix I. The following outline lists the characteristics and distribution of each *Speyeria callippe* subspecies. As noted by Arnold, the geographic variation of this species segregates into three major subspecies groups as defined below. However, significant variation also exists in each of these groups, particularly the Californian *callippe* group. One taxon, *S. callippe gallatini* (McDunnough), does not appear to have any distinguishing characteristics that separate it from *S. c. calgariana*, and is probably best regarded as a synonym of this latter taxon. Also, *S. c. sierra* must be regarded as a synonym of *S. c. juba* as previously discussed.

1.   *callippe* group — dorsal forewing with thick, dark veins in male, ventral hindwing with dark brown to yellow disc, spots silver or unsilvered, median spots pointed or rounded but not large and elongate, distinct yellow submarginal band.

2.   *semivirida* group — dorsal forewing with thin, light veins in male, ventral hindwing with greenish brown to brown disc, spots always silver, median spots very large and elongate, yellow submarginal band present or absent.

3.   *nevadensis* group — dorsal forewing with thin, light veins in male, ventral hindwing with green to gray disc, spots always silver, median spots very large and elongate, yellow submarginal band present or absent.

1a. *S. callippe callippe* (Bdv.) — dorsal wings with pale yellow-orange ground color combined with very extensive basal suffusion, ventral forewing with extensive reddish color in male, ventral hindwing with a brown disc covered with yellow suffusion, spots always silver, median spots pointed, narrow submarginal band.
     Distribution — San Francisco Bay area.

1b. *S. callippe comstocki* (Gunder) — differs from typical *callippe* in having reduced basal suffusion on dorsal wings, mostly yellow color on ventral forewing of males, and a mostly yellow disc.
     Distribution — inland and southern Coast Range from Contra Costa Co. to Baja California.

1c. *S. callippe macaria* (Edwards) — dorsal wings medium orange with almost no basal suffusion, ventral forewing of male with extensive reddish color, ventral hindwing with pale brown to yellow disc, spots usually silver (90% or more), median spots small and pointed, submarginal band very wide covering nearly a third of the hindwing.
     Distribution — Tehachapi Mts., Ventura Co. to Kern Co.

1d. *S. callippe laurina* (Wright) — differs from *macaria* only in having a high frequency of unsilvered spots (60% or more).
     Distribution — west slope Greenhorn Mts., Kern Co. to southern Tulare Co.

1e. *S. callippe inornata* (Edwards) — dorsal wings medium to ruddy orange with moderate basal suffusion, ventral hindwing with a light to dark, dull brown disc, spots usually unsilvered, median spots large, round to pointed, submarginal band narrow.
     Distribution — low foothills along Sierra Nevada west slope, Shasta Co. to northern Tulare Co.

1f. *S. callippe juba* (Bdv.) west slope race ("*laura*" phenotype) — differs from

inornata in having silver spots and a wide yellow submarginal band. Disc color light to dark brown.

Distribution — high elevations along the Sierra Nevada west slope, Tehama Co. to Placer Co.

1g.   *S. callippe juba* east slope race (*"sierra"* phenotype) — differs from the west slope race in having almost no basal suffusion on the dorsal wings, a very pale brown or yellow disc, often with a greenish tinge, and in having very small wing size (male forewing length usually 26-27 mm).

Distribution — high elevations along the Sierra Nevada east slope, Lassen Co. to Eldorado Co.

1h.   *S. callippe rupestris* (Behr) — differs from *inornata* in having dark ruddy orange ground color combined with very extensive basal suffusion on the dorsal wings. Ventral hindwing with a dark red-brown to dull brown disc, spots usually unsilvered (80% or more).

Distribution — northern Coast Range and Salmon-Trinity Mts., Mendocino Co. to Siskiyou Co.

1i.   *S. callippe liliana* (H. Edwards) — differs from *rupestris* and typical *callippe* in having only light basal suffusion; differs from typical *callippe* in having ruddy orange dorsal ground color, and a solid red-brown disc without much yellow suffusion; differs from *rupestris* in having silver spots.

Distribution — California Coast Range, Napa Co. to Glenn Co.

1j.   *S. callippe elaine* dos Passos & Grey — differs from *rupestris* in having a high frequency of silver spots (80% or more). Populations from Mt. Shasta to the Oregon Siskiyou Mts. have a dark red-brown to dull brown disc. Populations from the Oregon Cascade Range (west slope) have a dark slate-brown to jet black disc, often with greenish suffusion from Douglas Co. to Linn Co.

Distribution — northern Siskiyou Co. California to Linn Co. Oregon.

2a.   *S. callippe semivirida* (McDunnough) — dorsal wings pale yellow orange with thin veins in male, ventral hindwing with a light to dark disc, greenish brown to slate-brown, silver median spots very large and elongate, yellow submarginal band narrow or obliterated with brown suffusion.

Distribution — east slope of the Cascade Range from Klamath Co. Oregon to British Columbia, east through northern Idaho.

2b.   *S. callippe semivirida* "Columbia" race — differs from typical *semivirida* in having dark orange ground color on dorsal wings, and a dark red-brown to "chocolate" brown disc on ventral hindwing.

Distribution — south-central British Columbia.

3a.   *S. callippe nevadensis* (Edwards) — differs from *semivirida* in having a pale yellow-green disc and a distinct yellow submarginal band.

Distribution — foothills along Sierra Nevada east slope, eastern California from Lassen Co. to Inyo Co. east to western Nevada.

3b.   *S. callippe harmonia* dos Passos & Grey — differs from *nevadensis* in having the submarginal band obliterated with green suffusion. Disc color yellow-green, bright green, or gray-green.

Distribution — eastern Nevada, Utah, Idaho, western Colorado to western Montana.

3c.   *S. callippe meadii* (Edwards) — differs from *harmonia* in having considerable dark basal suffusion on the dorsal wings, disc color bright green to dark

olive-green.

Distribution — Colorado Front Ranges east of Continental Divide.

3d.   *S. callippe calgariana* (McDunnough) — differs from *harmonia* in having a high frequency of gray and gray-green discs, bright green or yellow-green colors usually scarce or absent.

Distribution — east of Continental Divide, Canadian prairies of Alberta to Manitoba, south to eastern Wyoming and western Nebraska.

The Biology and Morphology of the Immature Stages of *Asterocampa idyja argus* (Bates) (Lepidoptera: Nymphalidae)

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Abstract. The immature stages of *Asterocampa idyja argus* (Bates) (Lepidoptera, Nymphalidae, Apaturinae) are described for the first time from specimens collected in southern Mexico. An investigation of external characters of eggs, late instar larvae and pupae was carried out with the aid of scanning electron microscopy. A nomenclature for larval head capsule scoli is proposed. A new structure, the crampets, found on the prolegs of caterpillars, is described. *Celtis caudata* Planch. was found to be the larval host plant in southern Mexico. This is the first recorded host for this hackberry butterfly.

Introduction

Species of *Asterocampa* Röber (Lepidoptera, Nymphalidae, Apaturinae), known as hackberry butterflies, occur in North and Central America and the Greater Antilles. The developmental stages of 2 widely distributed species, *A. clyton* (Boisduval & Le Conte) and *A. celtis* (B. & L.), are known from populations in the eastern United States (Riley, 1874; Edwards, 1880, 1881, 1884, 1897; Scudder, 1889). Other populations of these two species from the southwestern United States, and the remaining two species of *Asterocampa* have received little attention (Comstock, 1953, 1961; Gundlach, 1881). Comstock described the mature larva and pupa of *A. leilia* (Edwards) from Arizona in 1953. However, the early instar larvae which he described as *A. leilia* actually belong to another species, *A. clyton texana* (Skinner) form "subpallida." The mature larva and pupa of *A. idyja idyja* (Geyer) from Cuba were described by Gundlach (1881), but were not illustrated.

Eggs, third, fourth and fifth instar larvae, and pupae of the Central American *A. idyja argus* (Bates) are described here for the first time from specimens collected in the states of Oaxaca and Guerrero, Mexico. Unhatched egg masses and early instar larvae were not observed or obtained through rearing.

Materials and Methods

MATERIAL COLLECTION AND REARING. The immature stages of

Asterocampa idyja argus were collected from their host trees during July of 1980 and 1981 in 2 localities in southern Mexico. A (partial?) clutch of third and pharate fourth instar larvae from near Cacuamilpa in northern Guerrero were the earliest instar larvae found. Hatched egg masses, fourth and fifth instar larvae, larval skins and head capsules, pupae and pupal cases were found in abundance near Totolapan in southeastern Oaxaca. Branchlets with evidence of larval feeding damage, leaves with silken larval resting pads or frass, and a few adult butterflies were also collected.

The majority of larvae and pupae were preserved immediately and the remainder reared for determination.

MATERIAL PREPARATION. Egg shells and larval head capsules were air-dried and mounted on scanning electron microscope stubs with a quick-drying plastic. After coating the eggs with gold/palladium, they were viewed with a JEOL, JSM-25SII scanning electron microscope. Some larval heads were removed, soaked in KOH at room temperature for a few hours, stained in mercurochrome, and cleaned with a brush. The parts were then cleared in clove oil, hardened in xylene and mounted on microscope slides in balsam. One third and one fifth instar larva were critical-point dried and prepared for scanning electron microscopy.

NOMENCLATURE. Color descriptions were made from direct observation of live and preserved specimens and from color photographic slide transparencies taken of live material. Color names are those used in ordinary description followed in parentheses (where different) by names in the National Bureau of Standards' color dictionary (Kelly and Judd, 1976).

Nomenclature used to describe the morphology of immature stages is taken from a variety of sources, including Kuznetsov (1967) and Razowski (1976). To describe head capsule structure and coloration in detail it was necessary to construct a new nomenclature of head horns, as no previous nomenclature existed. An attempt was made to use a terminology consistent with head capsule setal homology (Hinton, 1946), so as to permit phylogenetic analysis among caterpillars with homologous head capsule structure.

The paired, branching scoli (Figs. 1, 2) found at the dorsolateral corners of the head capsule are each termed "A," for "antler," as these are not homologous with any named primary seta. The branches of the antlers are named according to their location. Of the terminal forked pair of scoli the more lateral is designated "AL" and the more mesal "AM." Other scoli associated with the terminal pair are designted by the prefix "AT," and numbered from the posteriormost towards the meson around the antler (clockwise as viewed dorsally for the right antler). There is one (AT1) in *Asterocampa*. Scoli more basad on the trunk of the antler are
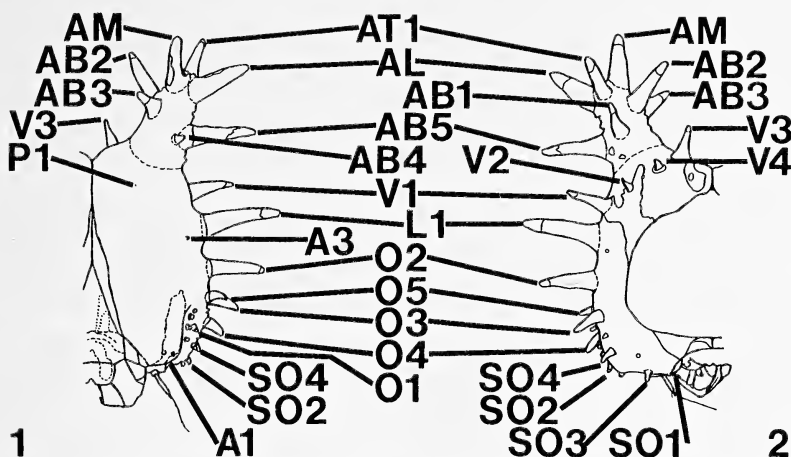
Figs. 1 & 2.   Head of mature larva with major scoli labelled: **1,** front view; **2,** back view.

designated by the prefix "AB." They are numbered in a similar manner, from the posteriormost towards the meson around the antler. There are 5 in *Asterocampa* (AB1, AB2, AB3, AB4, AB5).

Some of the unbranched scoli of the cranium are homologous with primary setae named by Hinton (1946) (as determined in developmental sequences in other *Asterocampa* species). The prominent pair of scoli on the vertex is the dorsalmost pair of vertical setae (V3). A similar pair of scoli on the occiput, just ventral to the antlers in frontal view, is the ventralmost pair of vertical setae (V1). The top pair of long lateral scoli are the lateral setae (L1). The next lower pair of lateral scoli are the second ocular setae (O2). The next lower pair of lateral scoli on the occiput are the third ocular setae (O3). The first ocular setae (O1) appear as scoli just lateral to the arc-forming simple eyes. Subocular setae SO2 and SO3 appear as scoli behind and below the eyes as figured. On the face of the larva only the first and third anterior setae (A1, A3) appear as scoli and these are very small. The first pair of parietal setae (P1) are found at the anterior bases of the antlers.

Several scoli of the vertex and subocular regions have no corresponding primary setae. These secondary scoli are designated by the prefix of their cranial areas and numbered in order of their appearance during larval development (numbers beginning beyond those given to primary setae; see Figs. 1, 2).

Observations on the Biology of the Immature Stages of *A. idyja argus*

HOSTS. The host plant species from which the immature stages of *Asterocampa idyja argus* were collected is *Celtis caudata* Planch. The

determination of this plant was made using the key to species of hackberry in Mexico by Standley (1922). The tree occurs only in the central part of the range of the butterfly. *A. idyja argus* is found from northwestern Mexico to Nicaragua, with an extension into northeastern Mexico (corresponding well with the Mexican Biotic Province, as illustrated in Durden, 1974).

Immature stages of *A. idyja argus* were located subsequent to finding larval feeding damage. The characteristic feeding damage on trees is the best indication of the presence of larvae. Typical damage is illustrated by the figures of pressed leaves collected in Oaxaca (Figs. 3-5).

3   **4**   **5**
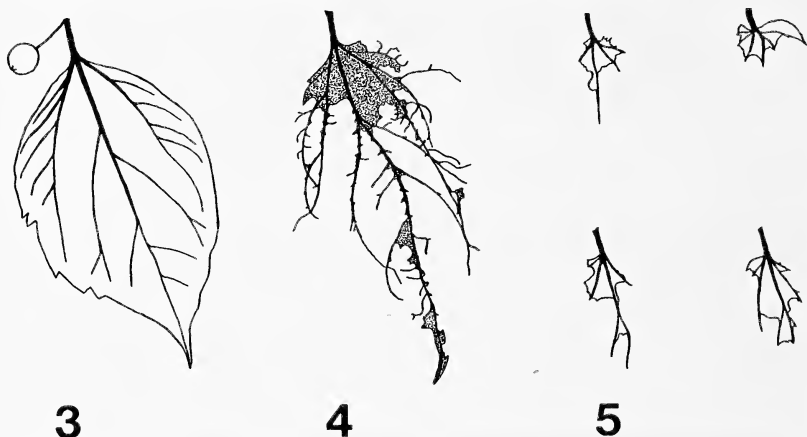
Figs. 3-5.   Leaves of *Celtis caudata* **3,** undamaged leaf with fruit, showing major veins; **4,** leaf fed upon by early instar larvae; **5,** leaf remains after feeding by late instar larvae.

EGGS. Two hatched egg masses were observed on terminal branchlets which showed larval feeding damage in the lateral canopy of one host tree. One of these was accessible and was collected. This egg mass is composed of (the remains of) 5 layers of closely packed egg shells (hexagonally close-packed). The outermost eggs remained intact because they were mostly parasitized by scelionid wasps (*Telenomus* sp.), and were not removed by emerged larvae. Eggs inside the mass are absent probably as a result of being dislodged and eaten by emerging larvae. As calculated from the stacking design there were 103 eggs in the bottom layer, and maxima of 85 in the second, 68 in the third, 52 in the fourth and 38 in the fifth and top layer. As a conservative estimate, the egg mass probably contained in excess of 300 eggs when deposited.

LARVAE. More than 200 third and pharate fourth instar larvae were found on a single leaf and adjoining stem on the host plant in Guerrero. The larvae were massed for molting near the tip of an exposed, hanging branch which exhibited extensive feeding damage.

Fourth, pharate fifth, and fifth instar larvae were found mostly inside the canopy of the host tree where many mature larvae were feeding. Larvae resting on the undersides of leaves assumed zigzag positions (body bent laterally twice), similar to illustrated larvae of *Timelaea maculata formosana* Fruhstorfer (Kubo and Muroya, 1967), another apaturine nymphalid. When not feeding, caterpillars tucked their head under, placing faces against the leaf, antlers to the front. Some mature larvae were found travelling along branches between leaf clusters, a few of them probably searching for pupation sites. Larvae swung their heads to the side and regurgitated food when handled.

PUPAE. Pupae and pupal cases were found on the same tree as mature larvae, on the undersides of leaves on branchlets very close to the main trunk and in the darkest shade within the canopy. Each pupa rested head downward with its longitudinal axis parallel to the leaf blade and its caudal end towards the petiole. The pupal stage lasted 7-8 days.

Description of the Immature Stages of *A. idyja argus*

Egg (Fig. 33). Egg whitish, typical of *Asterocampa*, 19 or 20 ribs, 0.80 mm wide by 0.85 mm high, deposited in large clusters. Micropylar rosette similar in design to that of *Apatura iris* (L.) (Friedrich, 1977), 6-8 petals; fovea centralis roughly triangular, micropylar openings at corners (occluded in figure).

Mature Larva (Figs. 1, 2, 6, 7, 9-13, 16-32). Fifth instar larva 3-4 cm long, male larvae 80% as long as females; body widest at middle, roughly 5 mm. Head 5 mm wide counting lateral scoli. Anal horns arising from dorsal plate, each 1 mm long.

Head (Figs. 1, 2, 10-13) mostly black, hairy, with whitish (yellowish white) patches on lower face and antlers posteriorly. Head capsule blackish with translucent areas through which tissues in living specimens appear whitish. Antler trunk, AB4, dark brownish black; AL concolorous anteriorly and at tip, but whitish posteriorly; AM dark only anteriorly on apical half. All other antler scoli whitish with dark brownish black tips, as are L1, O2 and V1. Other head scoli whitish, except in subocular region (SO1, SO3, brownish black). Whitish streaks mesad of ocular creases, ventrally to and including antennae. Frons whitish laterally on lower half, clypeus dark only at sides. Two pairs of whitish markings on occiput dorsally in lines extending back from antlers and back below each V3 scolus. Head appendages whitish to amber-colored (orange yellow), except black mandibles, brownish black basal portions of maxillae and labium, brown spinneret. Lower 3 simple eyes of arc-forming 4, ringed with black.

Body longitudinally striped with shades of yellow and green (olive), spiracles whitish. Anal horns black. Heart-line dark, olive black, centered dorsally, showing through unpigmented cuticle of body. Subdorsal bands broad, pale to light yellow, longitudinally bisected by intermittent medium olive line; outer (more lateral) portion of subdorsal band called dorsolateral band. Subdorsolateral bands olive black each with line of contrasting white chalazae more or less centered within and along dark olive center. Light yellow supraspiracular bands lateral to subdorsolateral bands. Spiracular bands olive with contrastingly light-colored spiracles
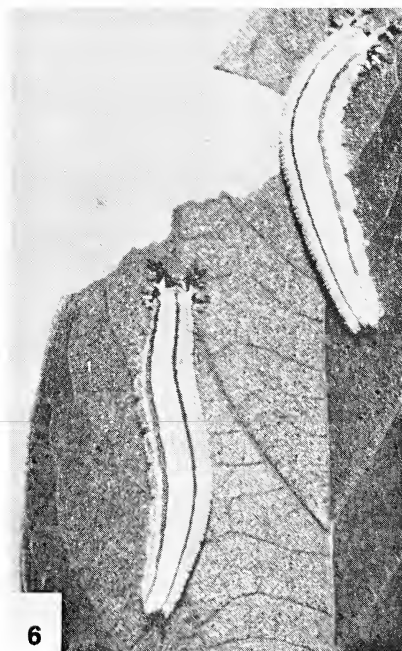
Fig. 6.   Larva: Fifth instar, dorsal view.
Fig. 7.   Larva: Fifth instar, lateral view.
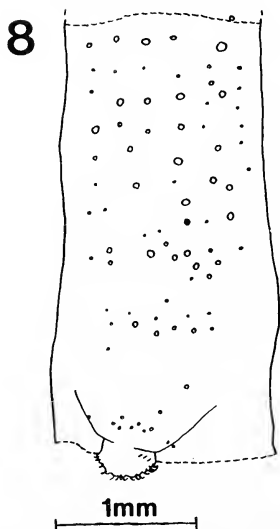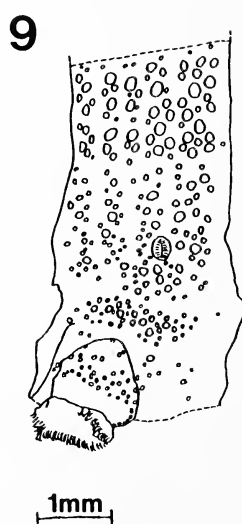
Figs. 8 & 9.   Lateral views of right, fifth abdominal, segment of larvae: **8,** third
                 instar; **9,** fifth instar.

centered within and along deep yellow center. Subspiracular bands light yellow. Below subspiracular bands, including prolegs, thoracic legs and venter, olive. In some specimens, yellow bands more intense (strong yellow). Green color leached from larvae in alcohol, pinkish hue (light yellowish pink) of muscles showing through cuticle. Yellowish pigment a particulate substance remaining where deposited under cuticle (uric acid?) and filling bases of chalazae. Light-colored developing wing buds (laterally under cuticle of meso- and metathorax) and testes (males, on either side of heart-line under cuticle, abdominal segment 5) visible in wet-preserved specimens.

Cranial sclerites joined along pitted suture lines. Median facial sclerite reaching only middle of face dorsally. Vertex bulging dorsally, lateral cranial hemispheres closely and broadly appressed above epicranial suture hidden between. Face coarsely, evenly pitted dorsally at sides of epicranial suture, pits up to vertex, over to occiput. Another field of pits from bases of antlers, broadening towards simple eyes, surrounding large lateral scoli, but distant from adfrontal sutures. Pits reflect sites of mandibular muscle fiber attachment, fibers not extending inside head scoli or antlers. Head appendages (antennae, mouth parts) illustrated (Figs. 16-25).

Body integument shagreened, studded with white chalazae with colorless setae. Chalazae scattered over membranous cuticle, forming clumps defined by musculature, body segments and annuli. Membranous cuticle of body finely spiculiferous. Setae borne on chalazae above spiracular band generally short and blunt, those below acute and longer. Fused chalazae form plates at either side of pronotum anterodorsal to spiracles, rarely fused elsewhere.

Prothorax with 2 abutting dorsal plates studded with short, blunt setae borne on chalazae. Ventral prothoracic gland opening in broad, transverse slit anteromesad of prothoracic legs, internally a bilobed membranous sac with lobes each less than 1 mm long. Meso- and metathorax with 4 annuli each. Thoracic legs (Figs. 26, 27) smoothly sclerotized, covered with long setae, claws appendiculate.

Spiracles covered by sieve plates (Srivastava, 1975) composed of ciliated extensions of rim, posterior ones external, overlapping tips of those attached anteriorly.

Abdominal segments 1 and 2 with 4 annuli; segments 3-7 with 5 annuli; segment 8 with 3 annuli. Ninth abdominal segment narrow, bordering anal plate (Figs. 28, 29) dorsally. Plate beaded between chalazae as in pronotum. Prolegs (Figs. 30-32) with 3-ranked mesoseries of amber-colored (orange yellow) crochets, 90 per proleg, each striated longitudinally. Field of tiny, sclerotized hooks, named here **crampets** (meaning "tiny hooks," in the sense of "crampons," the climbing hooks of mountaineers), on mesal surface of proleg planta. Crampets individually "T"-shaped or spade-shaped, curving in same direction as crochets, probably for clasping silk. As the crampets occur mesally on the prolegs their action is probably more like Velcro[R] than like the adhesion surfaces of the feet of house flies.

Third and Fourth Instar Larvae (Figs. 8, 14, 15). Larvae of these instars do not differ in any major way from mature larvae except in size. Some characters are compared in Table 1.

Head capsules of third and fourth instar larvae (Figs. 14, 15) maintain their integrity after being shed. Those of the fifth instar separate along the epicranial and adfrontal sutures. The pattern of light markings on the head differs slightly in

these instars. There is more white on the face and occiput dorsally in earlier instars than on the black head of the fifth instar. The antlers of the third instar are uniformly brownish black. Third instar larvae are lighter shades of green (olive) and yellow on the body, except for the heart-line; fourth instar larvae look like fifth instars in color. Third and fourth instar larvae have proportionally fewer chalazae and setae than fifth instar larvae.

Table 1.   Comparison of larval characters among late instar *Asterocampa idyja argus* larvae.

Character (millimeters)	**Instar 3**	**Instar 4**	**Instar 5**
Body length (maximum)	13	*	30-40
Body width (maximum)	2	*	5
Head width (excluding scoli)	1.5	2.67	4.0
Antler length	0.15	1.2	1.9
Prothoracic spiracle height	0.16	0.44	1.0
Crochets/proleg (number)	30	40	90

*No data on maximum

Pupa (Figs. 34-36). Pupa typical of *Asterocampa*, 2.1-2.6 cm long, 0.7-0.9 cm wide, 0.9-1.2 cm high at abdominal crest maximum (third abdominal segment), females larger than males. Head prolongations blunt, carinate dorsally. Antennae, bases of legs and galeae rugose externally, antennal segments corresponding to successive pairs of bumps. Pupal case splits dorsally along median carina from head, just behind antennae to posterior edge of mesonotum. Metanotum very narrow medially (longitudinally). Anterior median edges of third through eighth abdominal segment produced into spines. Prothoracic spiracles opening into transverse slits just above antennae. Wings completely covering first abdominal segment spiracles; hind wings partially covering spiracles, abdominal segments 2 and 3; eighth abdominal spiracles vestigial in appearance. Cremaster with long pad packed with hooked spines spines between carinae sustentorum; pad "Y"-shaped (Fig. 36), as in *Chitoria* (Muroya et al., 1967), another apaturine genus. Pupa leaf green (yellowish green) with whitish markings and very cryptic. Dorsal carinae of head prolongations, median dorsal carina from pronotum to third abdominal segment, lateral carinae along protruding edges of hind wings, major veins of fore wings, marked with whitish. Diagonal white stripes on sides of abdominal segments 2-7 between crest and spiracles, higher ends of stripes posterior; no subspiracular longitudinal stripes. Black spots on either side of spines on abdominal segments 3-8.

Discussion

Asterocampa idyja remains the least known species of hackberry butterfly. Biologically and morphologically the immature stages place the species in the Clyton Group of Skinner (1911), from which they can be separated from *A. clyton* geographically and morphologically. The black head and anal horns of the late instar larvae, as noted by Gundlach (1881), and the short metanotum of the pupa are diagnostic for *A. idyja*. The larval body is striped like some eastern larval populations of *A.*

clyton, but tending to more intense shades of yellow and green (olive). N. D. Riley's (1975) abbreviated description of the mature larva, presumably based on Gundlach's article, is in error in stating that the larvae have orange (instead of yellow, "amarilla" in Gundlach) longitudinal body stripes. It is hoped that *A. idyja idyja* will soon be described in sufficient detail for comparison with *A. idyja argus*, described here.

A population of *A. idyja argus* has recently been discovered in Sonora, Mexico, by collectors from Arizona. There is virtually no difference in morphology between this population and others in Mexico.

There is much work to be done on the biology of *A. idyja argus*. Different host plants should be encountered in the peripheral parts of the butterfly's range. In northwestern Mexico, the immature stages have been found on *Celtis reticulata* Torr., and in northeastern Mexico, one would expect them to be on *C. laevigata* Willd. In Guatemala, Honduras and Nicaragua the host tree is probably *C. trinervia* Lam., just as it is in the Greater Antilles for this species.

Interested field lepidopterists should search for gravid females and unhatched egg masses to get fresh eggs and early instar larvae for study. One would expect a variety of parasites and predators to be found associated with all the developmental stages of *A. idyja argus*, once the butterfly is better known.

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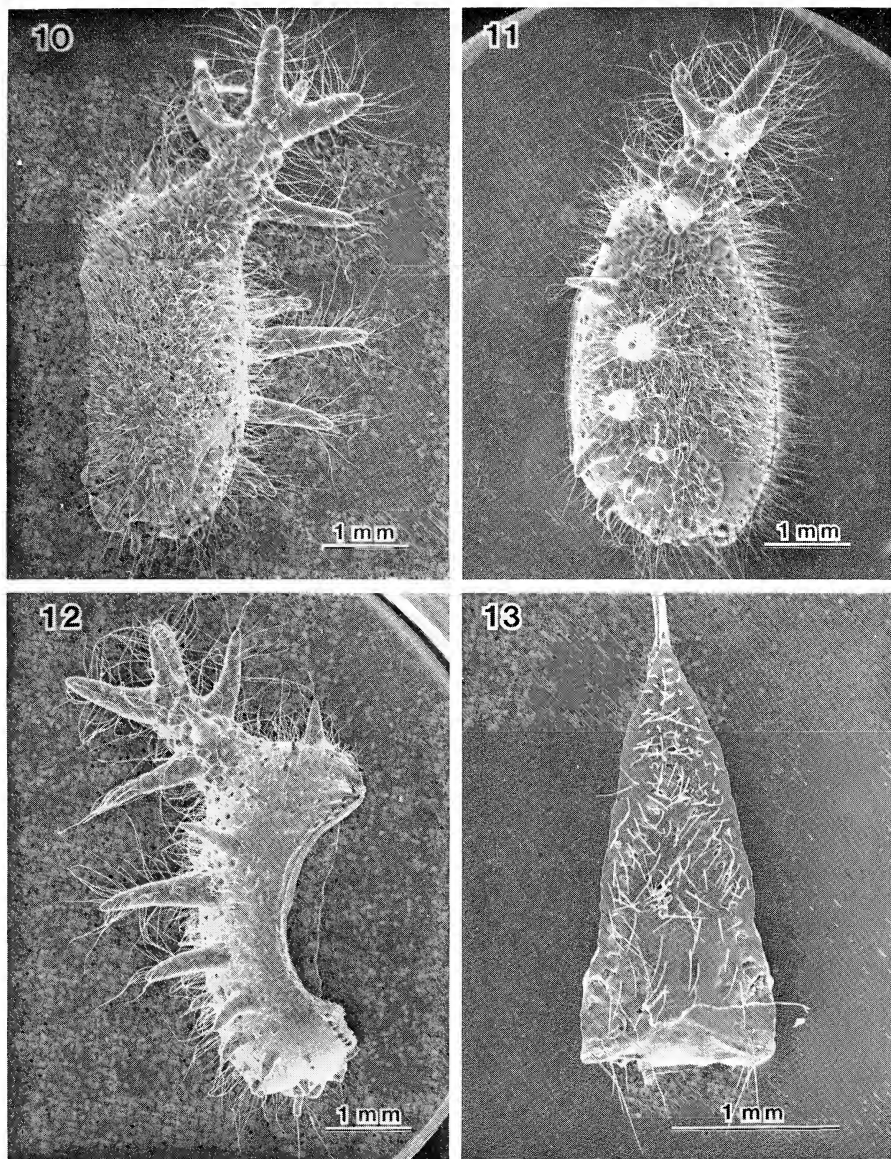
Figs. 10-13.   Head capsule of mature larva: **10,** left front; **11,** right side; **12,** left back; **13,** median facial sclerite, as shed (with labrum removed).
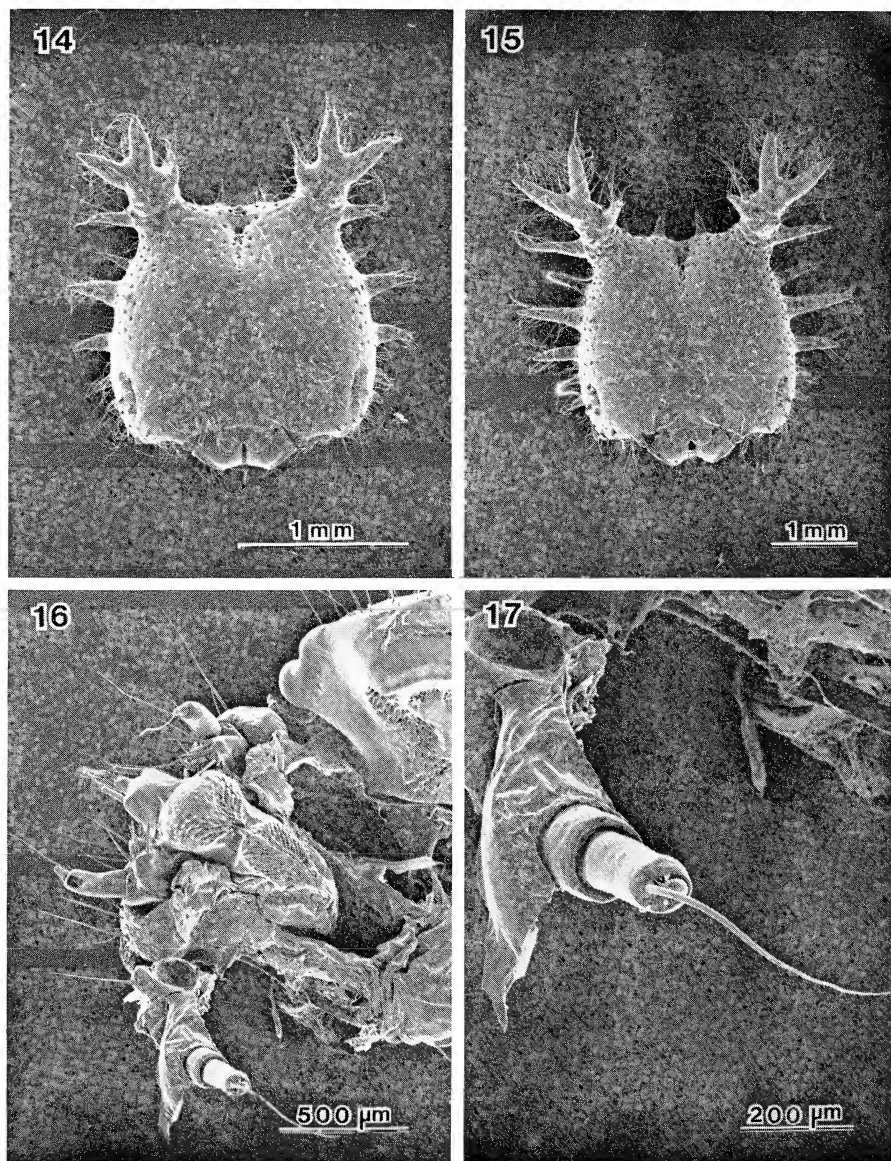
Figs. 14 & 15. Head capsules of larva: **14,** third instar; **15,** fourth instar.

Figs. 16 & 17. Head appendages of mature larva (left mandible, right antenna, not shown): **16,** front view (ventral to the left); **17,** left antenna (slightly collapsed at tip).
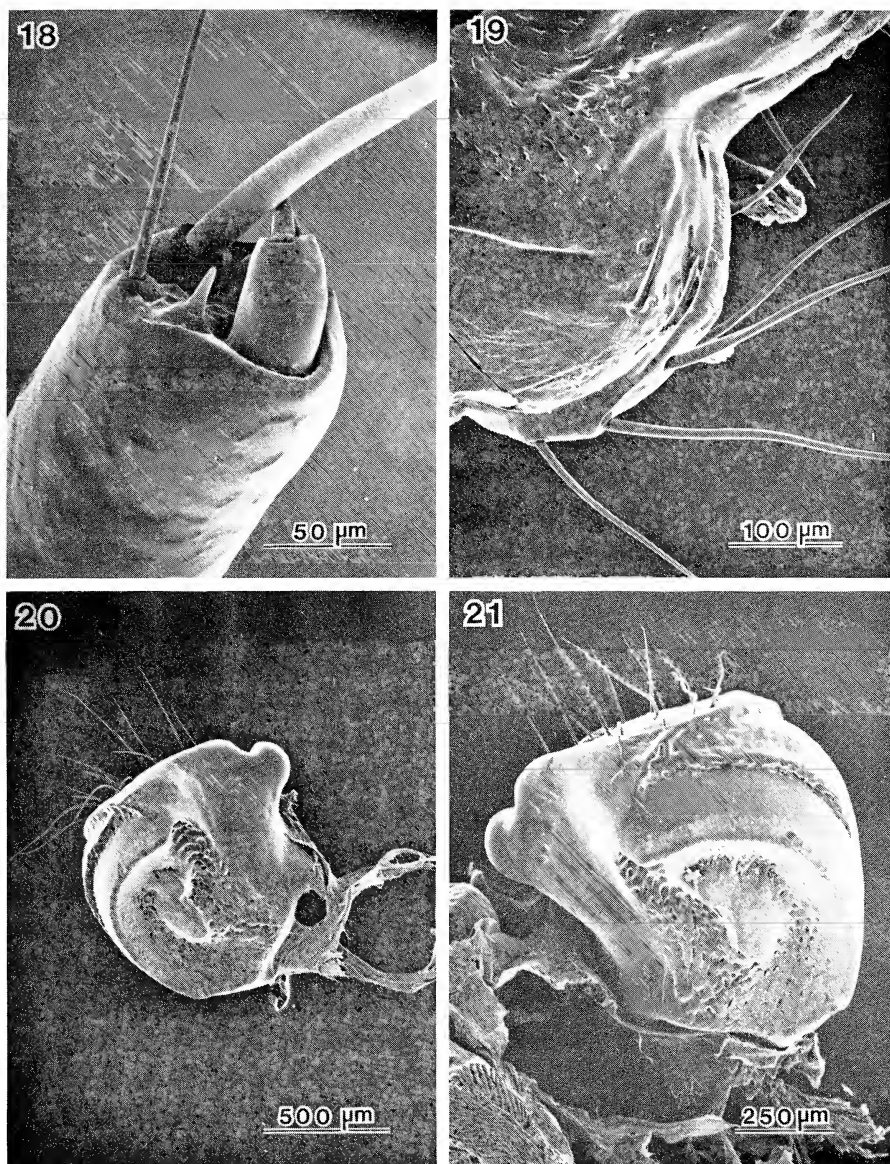
Figs. 18 & 19. Head appendages of mature larva (left mandible, right antenna, not shown): **18,** left antenna (slightly collapsed at tip); **19,** underside of labrum (note: minute cilia (found laterally), adoral spines, pores and setae).

Figs. 20 & 21. Mandibles of mature larvae: **20,** left; **21,** right.
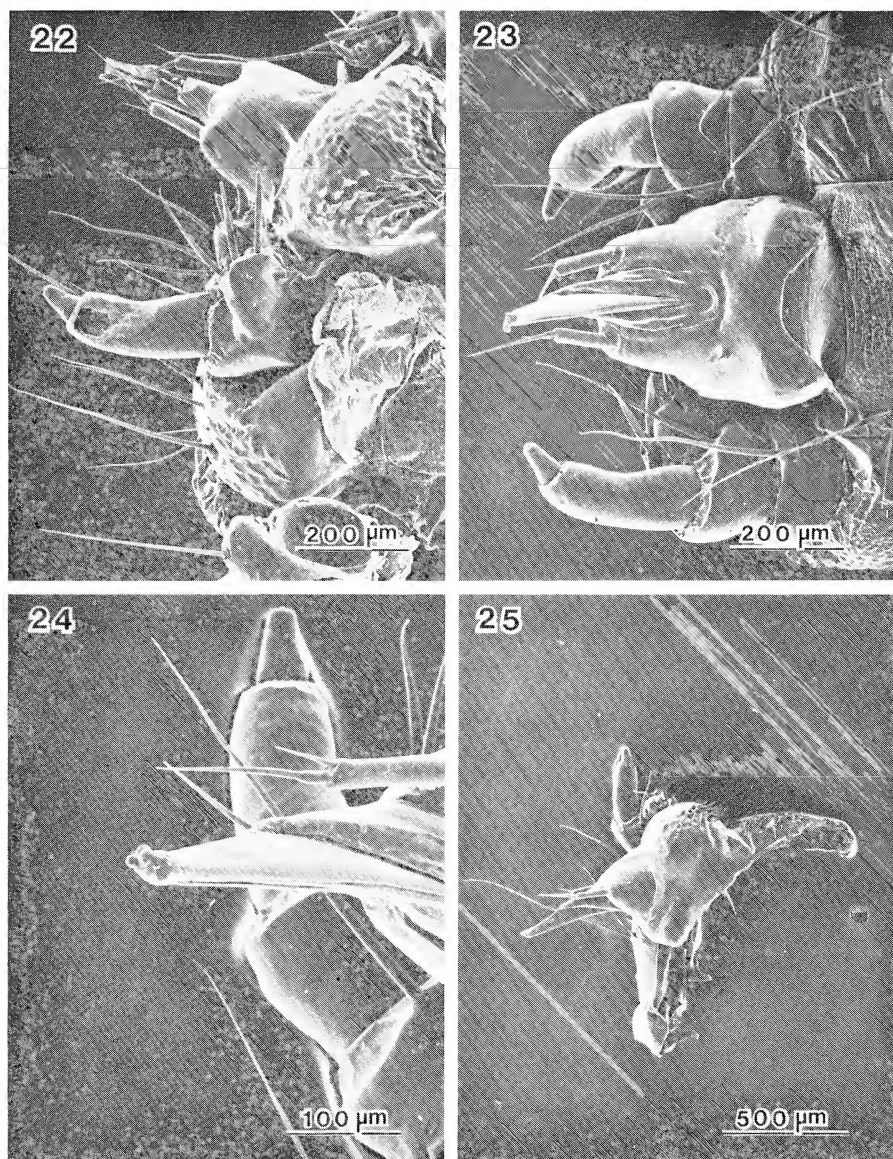
Figs. 22-25.   Maxillae, hypopharyngeal complex of mature larvae: **22,** anterior view (ventral to the left); **23,** posterior view; **24,** spinneret (note: terminal nobs); **25,** lateral view of hypopharyngeal complex (left maxilla removed).
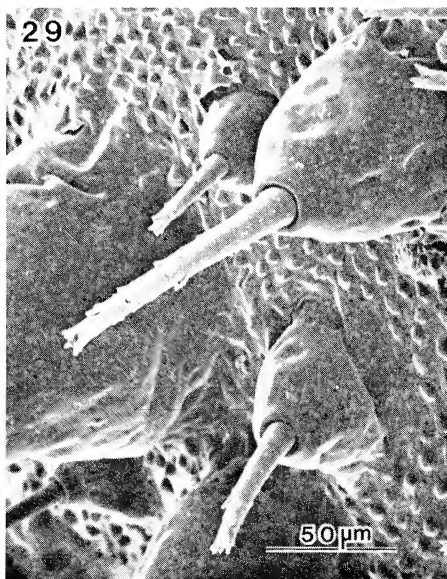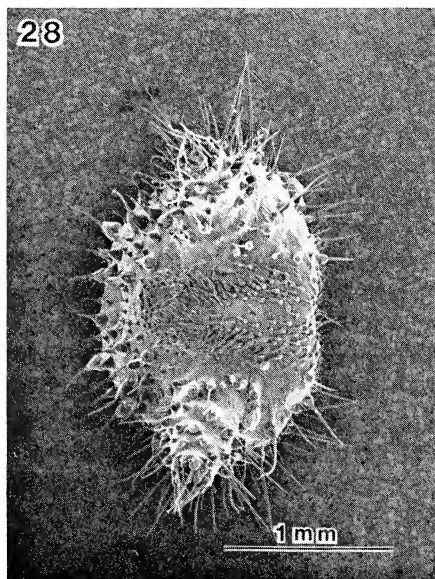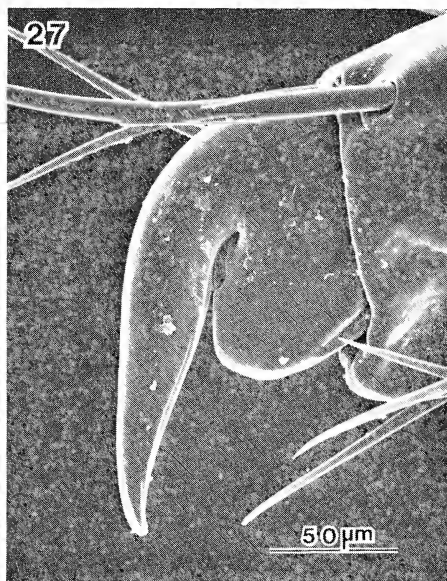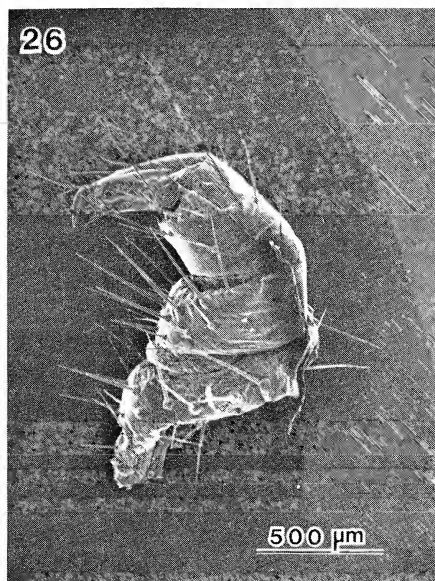
Figs. 26 & 27. Thoracic leg of mature larva: **26,** anterior view; **27,** claw.

Figs. 28 & 29. Anal plate of mature larva: **28,** posterior view (ventral to the right); **29,** dorsal chalazae (note: short-branched nature of setae, beaded texture of cuticle between chalazae).
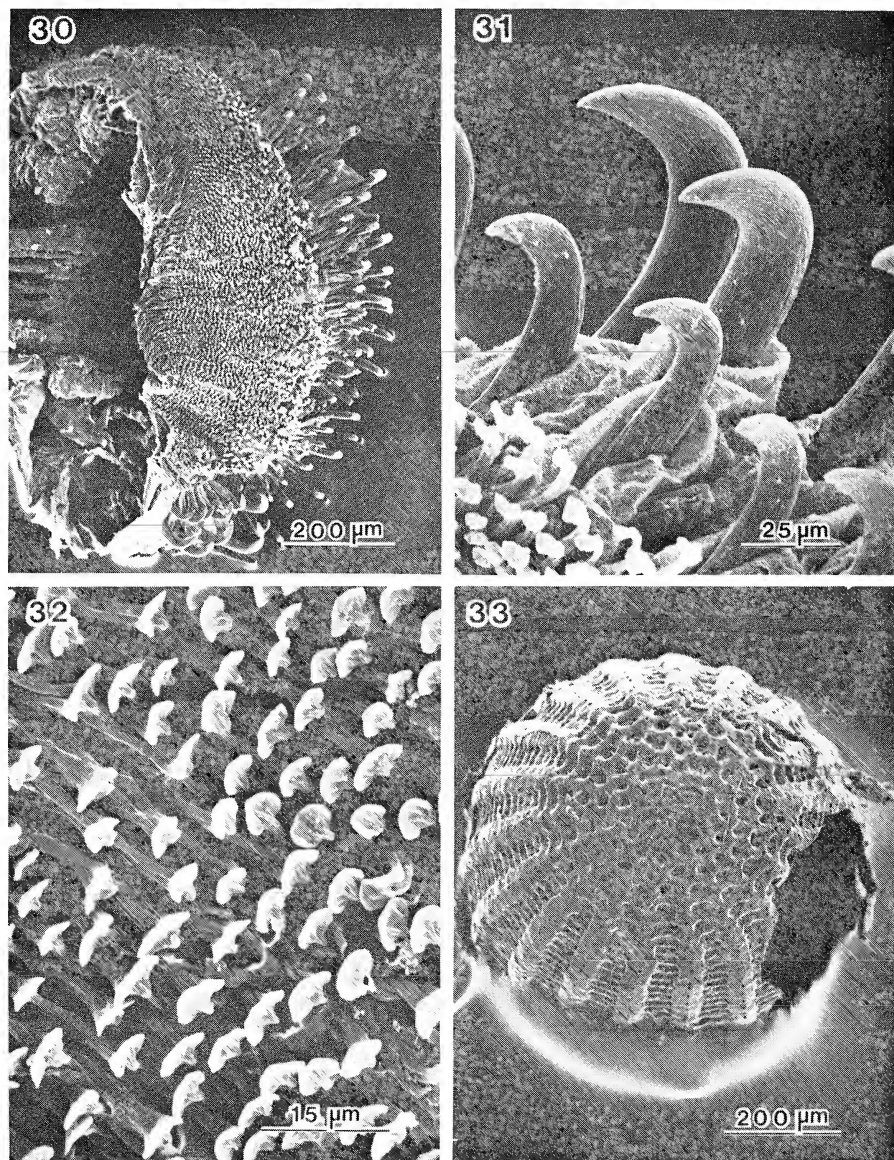
Figs. 30-32.   Fourth, right abdominal proleg of mature larva: **30,** mesal surface; **31,** crochets; **32, crampets.**

Fig. 33.   Egg: Dorsal view (note: exit hole made by scelionid parasitoid).
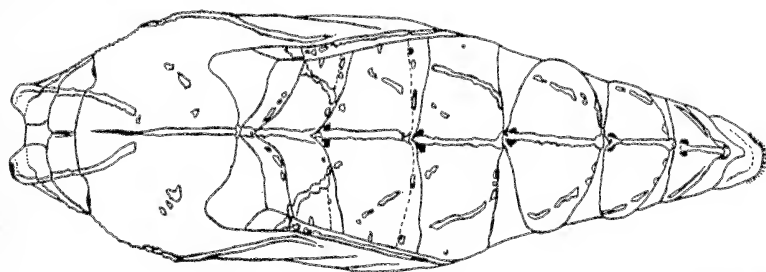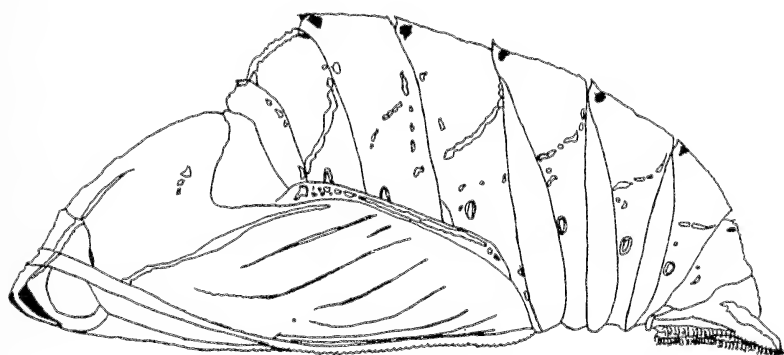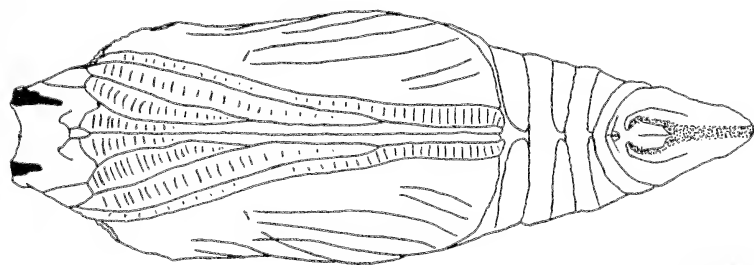
Figs. 34-36.   Pupa: **34,** dorsal view; **35,** lateral view; **36,** ventral view.

An Annotated Catalogue of the Burnets and Foresters (Lepidoptera: Zygaenidae) Named by Roger Verity

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Abstract. Species-group and infrasubspecific taxa of the family Zy-gaenidae named by R. Verity (1883-1959) are listed, with bibliographical data, information on their type-material, and notes on their status and/or identity. Proposals are made as to the stabilization of their nomenclature.

The present paper represents the third, and last, part of a series intended to provide students of Lepidoptera, particularly taxonomists, with annotated catalogues of the numerous taxa named by R. Verity, in all nearly 2000 names. The first (Kudrna, 1983) of the two already published papers dealt with the Papilionoidea (over 1500 names), the second (Kudrna & Balletto, 1984) treated the Hesperiidae (over 200 names). Like both previously published works, this is based on the study of both Verity's publications and the type-material preserved at the University Zoology Museum in Florence, Italy (Museo Zoologico de la Specola, Via Romana 17, I-50125 Firenze, Italy). Reference is also given to important publications which dealt with the taxa named by Verity, such as Naumann (1983) and Reiss & Tremewan (1967).

Whatever was said by Kudrna (1983) in the introduction to his catalogue of the butterflies is applicable also to Zygaenidae. Readers seeking information on Verity's collection, his life and work, as well as his bibliography, should also turn to the following publications: Baccetti, 1963; Beer, 1960; Kudrna, 1976, 1982 and 1983.

The main issue raised by Kudrna (1983) was judgment in respect to the availability (or unavailability) of Verity's names proposed in trinominal combinations for races, as a distinct taxonomic category, under the present condition set out in the current International Code of Zoological Nomenclature (edition 2, with all emendation valid at present). On further analysis of Verity's publications, Kudrna (1983) demonstrated that Verity's races are formally unavailable, having been published explicitly or implicitly in quadrinomy (cf. also Kudrna & Balletto, 1984). The study of Verity's works on the Zygaenidae has confirmed Kudrna's (1983) conclusions.

It may be interesting to summarize here what could be called the evolution of Verity's taxonomic concept, on the basis of the differential treatment of infraspecific taxonomic categories he chose to prefer at different times.

In 1911, while publishing the systematic index to the first volume of his never completed work "Rhopalocera Palaearctica", Verity treated his race unequivocally as an infrasubspecific category, denoted by a quadrinomen in case of all polytypic species, and a trinomen in case of all monotypic species. Later, until about 1920, Verity's view of "race" became inconsistent. He often then reverted to trinominals to denote races he otherwise used to treat in quadrinominal combination (e.g. *Zygaena filipendulae* race *calabra* Verity, 1917), or else he made use of infraspecific categories other than race (e.g. *Zygaena erythra* var. *albipes* Verity, 1916). After 1920, however, Verity became convinced of a new form of his own personal concept of polytypic species. This resulted in multinominal combinations such as *Zygaena ephialtes ssp. ephialtes razza albaflavens* Verity, 1920; or *Zygaena lonicerae* ssp. *trifolii* race *decreta* Verity, 1926, becoming characteristic and customary in his work.

In the later 1920's Verity became more and more convinced that his own subspecies concept was actually distinct from that of all other taxonomists studying the butterflies and moths. Subsequently, he substituted for subspecies a new taxonomic category which he called the exerge (Verity, 1925), in his Italian papers spelled eserge. In practical terms this was a change in terminology, rather than in meaning, of the then commonly used subspecies. Nonetheless, Verity (1925) claimed that the subspecies concept had over the years become exceedingly confused and that the subspecies concept was not adequately clear from the beginning. He proposed, therefore, that infraspecific taxa should be divided into two principal groups: the exerge and the race. Nevertheless, Verity published during this period only one new name specifically proposed for an exerge: *Zygaena fulvia* eserge *caledoniae* Verity, 1930.

It must be stressed at this stage, however, that Verity never made a constant use of his taxonomic categories, including his subspecies and his exerge. In his opinion, while some species were made of different exerges, others were not, constituting possibly just a single exerge. It certainly is not insignificant in this context that several of the subspecies, or exerges, formerly recognized by Verity are now considered to be taxonomically distinct species, or at least sibling species. For those species that Verity considered to be monotypic, or consisting of a single exerge (subspecies), he published new races in trinominal original combinations, such as *Zygaena carniolica* razza *anzascana* Verity, 1930; and *Zygaena purpuralis* race *isarica* Verity, 1922.

After about 1940, Verity gradually restricted the taxonomic (and

nomenclatorial) status of his exerges. He used the term as an indication of their supposed biogeographical origin instead of a zoological (latin) name (e.g. northern exerge, southern exerge, central exerge, etc.). He did this even for taxa with existing zoological (latin) names, usually of subspecies rank. In this way, the unique "exerge-concept" lost its original meaning and became closer to what is usually called "Rassenkreis" in the German literature.

The above represents, with some exceptions and inconsistencies on Verity's part, a brief outline of the evolution of his way of judging taxonomic categories within the species. One of such exceptions is the use of subspecies as late as in 1926 for a new taxon: *Zygaena lonicerae* subspecies *transferens* Verity, 1926. However, such cases do not imply that in order to assess the availability of a particular name given by Verity to a race, one must always try to discover what he thought at the time of naming the taxon. The very fact that Verity utilized intermediate taxonomic categories (subspecies and exerges) between specific and racial names is enough to treat all racial names as infrasubspecific for the purpose of zoological nomenclature. Any other attempt is bound to result in the most singular and subjective conclusions.

At the same time, it must now be recognized that Verity's names of races have become widely used and treated as subspecies by most subsequent authors. Additionally, it must not be overlooked that some subsequent authors (e.g. Reiss & Tremewan, 1967) "validated" Verity's racial names by completely ignoring the fact that they were published in unequivocal quadrinominal original combinations (of which they must have been aware). An example is the case of *Zygaena lonicerae* subspecies *lonicerae* race *minuens* Verity, 1926, which became subspecies *Zygaena lonicerae minuens*, in their catalogue (i.e. Reiss & Tremewan, 1967). Regrettably, the International Code of Zoological Nomenclature: Article 10(b) is rather ambiguous on the subject of the proper validation of an originally infrasubspecific name subsequently raised to the rank of the species-group name. Article 10, if broadly interpreted, insures that practically any quotation of an infrasubspecific name at species or subspecies rank, in no matter how obscure a faunal list, can consitute validation of the name. It seems to us that undertaking a thorough search of literature published over the past 70 years in order to ascertain who may have possibly validated a number of the 2000 names proposed by Verity would be a long and tiresome task. The effort not only fails to contribute to the advancement of lepidopterology, but indeed, would divert valuable time. There are many more fruitful tasks than sorting out a few names which are likely to contain a good measure of subjective synonyms.

With this in mind we wish to repeat here the plea already made by Kudrna (1983) and Kudrna and Balletto (1984), addressed to the International Commission on Zoological Nomenclature, requesting the use of

its plenary powers to rule that all names proposed by R. Verity for races are available names so long as they satisfy other relevant articles of the International Code on Zoological Nomenclature (cf. Kudrna, 1983). The names concerned were specified by Kudrna (1983) and Kudrna and Balletto (1984) by marking them with an asterisk and can be very briefly characterized as races with trinominal original combinations.

In the following catalogue, names are arranged in alphabetical order, each entry consisting of: caption (abbreviated original rank)—original combination author, year—bibliographical reference—type-material (if found) or type-locality (if known) or relevant information—comments and/or taxonomic history. Original taxonomic categories are abbreviated as follows: sp = species; ssp = subspecies; ex = exerge (eserge); ra = race; sf = seasonal form; if = individual/infrasubspecific form, aberration; sr = subrace; nn = nomen novum; hy = hybrid; nomen nudum is never abbreviated. Captions are printed: (1) in capitals for names originally intended for species-group taxa (i.e. species, subspecies, exerge and their replacement names); (2) in lower case preceded by asterisk for trinominal Verity's "race" recommended for subspecies-rank (see above); and (3) in lower case without asterisk for unavailable names (e.g. infrasubspecific taxa). Text placed in square brackets is our own, intended to supplement incomplete original data, which are taken directly from specimen labels and/or Verity's original designations. Unlike the publication on the butterflies and skippers, Verity, in his papers on Zygaenidae, usually interrupted the original combinations by inserting technical terms denoting infraspecific taxonomic categories; we have decided to repeat them, but as they do not form true parts of original combinations, we have placed them between inverted commas, as quotations.

acumine (if)—*Zygaena fulvia* 'forma' *acumine* Verity, 1930—Memorie Soc. ent. ital. 9:20—Type-locality not known.—Reiss & Tremewan (1967): *Zygaena loti tuscomodica acumine* (ab.).

acutafibra (if)—*Adscita alpina* 'forma' *acutafibra* Verity, 1946—Redia

31(1945/46):149—Italia ceentrale: Piceno: Massiccio Sibillini: Bolognola: 1200 m: 28 V 1913 Querci [leg.]; slide no. 527.

*aeris (ra)—*Adscita geryon* 'razza' *aeris* Verity, 1946—Redia 31(1945/46):154—Syntypes 1 male, 1 female [S. France]: A[lpes-]M[aritimes]: St. Barnabe: 1000 m: 28 V 1933: coll. Gazel.

albaflavens (ra)—*Zygaena ephialtes* 'sottospecies' *ephialtes* 'razza' *albaflavens* Verity, 1920—Boll. Lab. Zool. gen. agr. R. Scuola Agric. Portici 14:39—Syntypes 3 males, 12 females Italia centrale: Lucca: Prato Firito: 24-31 VII 1915: Querci [leg.]; 10 males, 7 females S[ud] Italia: Valle Mollarino: 500 m: 25-30 VII 1919: Querci [leg.]; 1 male ibid. M[on]te Meta: 900 m: 10 VII 1911.—Reiss & Tremewan (1967): *Zygaena ephialtes albaflavens* [nec Verity] (ssp.).

albarubens (ra)—*Zygaena ephialtes* 'sottospecie' *ephialtes* 'razza' *albarubens* Verity, 1920—Boll. Lab. Zool. gen. agr. R. Scuola Agric. Portici 14:39—Type-locality not known.—Reiss & Tremewan (1967): *Zygaena ephialtes albarubens* [nec Verity] (ssp.): the authors were in error considering the name to have been first published as nomen nudum and subsequently referring a later date: 1946.

ALBIPES [ssp]—*Zygaena erythra albipes* 'n.var.' Verity, 1916—Bull. Soc. ent. Fr. 1916:289—Syntypes 9 males, 1 female [Italy: Sicily]: Palermo: coll. Taormina; 4 males, 1 female Sicilia: Sevara: 5 VI 1928; 2 females Silcilia: S. Onofrio: 28 V 1928; 1 male [Sicily]: Trabsia; 1 male [Sicily]: M. Pellegrino: 18 V [1]930; 1 female Sicilia: Maridello [poorly legible: ?]: 10 VI [????].—Reiss & Tremewan (1967): Junior subjective synonym of *Zygaena erythrus saportae* Boisduval, 1829.

albovittata (if)—*Zygaena rhadamanthus* 'subspecies' *rhadamanthus* 'race' *oxytropiferens* 'f[orm]' *albovittata* Verity, 1920—Entomologist's Rec. J. Var. 32:161—A name proposed for an individual form described by Oberthuer (1910) in Etud. Lepid. comp. 4:592 found in some specimens from France: Alpes-Maritimes (Dept.)—Reiss & Tremewan (1967): *Zygaena rhadamanthus oxytropiferens albovittata* (ab.).

alpicola (nn)—*Zygaena loti* 'subspecies' *transalpina* 'race' *alpicola* Verity, 1920—Entomologist's Rec. J. Var. 32:29—Replacement name for *Zygaena loti alpina* Boisduval, 1834, said to be primary junior homonym of *Zygaena filipendulae alpina* Boisduval, 1834, but contrary to the rank of that name proposed in a quadrinominal original combination.—Reiss & Tremewan (1967): Junior synonym of *Zygaena transalpina alpina* Boisduval, 1834.

alpiumgigas (nn)—*Zygaena lonicerae* 'subspecies' *lonicerae* 'race' *alpiumgigas* Verity, 1926—Entomologist's Rec. J. Var. 38:73—Replacement name for *Zygaena lonicerae major* Frey, 1880, said to be junior homonym of *Zygaena filipendulae major* Esper, 1797, but contrary to the rank of that name proposed in quadrinominal original combination.—

Reiss & Tremewan (1967): *Zygaena lonicerae alpiumgigas* [nec Verity?] (ssp.).

*alpiummicans (ra)—*Zygaena fausta* 'race' *alpiummicans* Verity, 1926—Entomologist's Rec. J. Var. 38:106—Syntypes 24 males, 31 females [Italy: Piedmonte]: Alpi Cozie: Val di Susa: Oulx: 2-17 VIII 1925: Verity [leg.]—Reiss & Tremewan (1967): *Zygaena fausta alpiummicans* (ssp.).

alpiumnana (if)—*Zygaena lonicerae* 'subspecies' *trifolii* 'form' *alpiumnana* Verity, 1925—Entomologist's Rec. J. Var. 37:47; pl. 8, figs. 88-90.— Syntypes 2 males, 1 female [N. Italy]: Suedtirol: [Isarco Valley: road from Waidbruck to Castelruth]: 191[?]: Wagner [leg.].—Reiss & Tremewan (1967): *Zygaena lonicerae glaciei alpiumnana* (ab.).

angelicaeformis (if)—*Zygaena filipendulae* 'race' *alpina* 'form' *angelicaeformis* Verity, 1921—Entomologist's Rec. J. Var. 33:109—[S. France: Hautes Alpes]: Digne—Reiss & Tremewan (1967): *Zygaena filipendulae oberthueriana angelicaeformis* (ab.).

*anomala (ra)—*Adscita statices* 'razza' *anomala* Verity, 1946—Redia 31(1945/46):152; pl. 7, fig. 16; pl. 8, fig. 28—Holotype 1 male [S. France]: A[lpes] M[aritimes]: Le Borion: 1450 m: 18 VII 1935: coll. Gazel.

anticeconjuncta (if)—*Zygaena transalpina emendata anticeconjuncta* Verity, 1916—Boll. Soc. ent. ital. 47:77—[Italy]: Macerata—Name proposed for a specimen in Oberthuer's collection, no. 137.—Reiss & Tremewan (1967): *Zygaena transalpina emendata anticeconjuncta* (ab.).

*anzascana (ra)—*Zygaena carniolica* 'race' *anzascana* Verity, 1930— Memorie Soc. ent. ital. 9:22—Syntypes 20 males, 14 females [N. Italy: Alpi Pennine]: Vanzone: 700 m: 10 VII [19]24, 17-19 VII 1928: Verity [leg.]—Reiss & Tremewan (1967): *Zygaena carniolica anzascana* (ssp.).

apicejuncta (if)—*Zygaena stoechadis dubia apicejuncta* Verity, 1916— Boll. Soc. ent. ital. 47:74—[Italy]: Macerata—Reiss & Tremewan (1967): *Zygaena filipendulae major apicejuncta* (ab.).

aterrima (ra)—*Zygaena filipendulae* 'subspecies' *stoechadis* 'race' *aterrima* Verity, 1921—Entomologist's Rec. J. Var. 33:128—Syntypes 22 males, 16 females Italia centrale: Toscana: Palazzuolo Romagna: 700 m: 3-' VII 1917: Querci [leg.]—Reiss & Tremewan (1967): *Zygaena filipendulae aterima* [nec Verity] (ssp.).

*austronubigena (ra)—*Anthrocera (Mesembrinus) purpuralis* 'razza' *austronubigena* Verity, 1946—Redia 31:58—Lectotype male, Paralectotypes 3 males, 8 females (Naumann, 1983) [Italy]: Abruzzi: Gran Sasso: 1300-1500 m: 1939: Romei [leg.].—Reiss & Tremewan (1967): *Zygaena purpuralis austronubigena* (ssp.).

aureoviridis (if)—*Procris cognata* 'f[orma]' *aureoviridis* Verity, 1946—Redia 31(1945/46):134—Syntype 1 male [Italy: Emilia]: Ravnica: 20 VI 1919.

autumnalis (sf)—*Zygaena lonicerae major autumnalis* 'nom.nov.' Verity, 1916—Boll. Soc. ent. ital. 47:73—Syntype 1 male Italia centrale: Macerata: Monti Sibillini: Bolognola: 2 IX 1915: Querci [leg.]—Reiss & Tremewan (1967): *Zygaena lonicerae pauperetincta autumnalis* (f.t.).

autumnalis (sf)—*Zygaena transalpina transalpina autumnalis* 'nom. nov.' Verity, 1916—Boll. Soc. ent. ital. 47:76—Syntypes 2 males, 1 female Italia centrale: Piceno: Massiccio Sibillini: 1200 m: 4 IX 1913: Querci [leg.]—Reiss & Tremewan (1967): *Zygaena transalpina emendata autumnalis* (f.t.).

barcina (ra)—*Zygaena rhadamanthus* 'subspecies' *rhadamanthus* 'race' *barcina* Verity, 1920—Entomologist's Rec. J. Var. 32:161—A name proposed for three specimens described by Oberthuer (1910) in Etud. Lepid. comp. 4:590; type-locality Spain: Barcelona.—Reiss & Tremewan (1967): *Zygaena rhadamanthus barcina* [nec Verity] (ssp.).

*bellissima (ra)—*Adscita alpina* 'razza' *bellissima* Verity, 1946—Redia 31:151—Syntypes 5 males, 1 female [N. Italy: Alpi Marittime]: Valdieri: VII 1898, 26 VII 1905, 2 VIII 1907, 14 VII 1911.

biconjuncta (if)—*Zygaena stoechadis dubia biconjuncta* 'nom.nov.' Verity, 1916—Boll. Soc. ent. ital. 47:74—Italy: Macerata.—Reiss & Tremewan (1967): *Zygaena filipendulae caeruleochsenheimeri biconjuncta* (ab.).

bimacula (if)—*Zygaena filipendulae* 'f[form]' *bimacula* Verity, 1921—Entomologist's Rec. J. Var. 33:147—Type-locality not known—Reiss & Tremewan (1967): *Zygaena filipendulae aterrima bimacula* (ab.).

brevicornibus (if)—[*Zygaena lonicerae*] 'subspecies' *lonicerae* 'race' *etruriae* 'form' *brevicornibus* Verity, 1925—Entomologist's Rec. J. Var. 37:117, pl. 8, figs. 73, 74—Italia centrale: Firenze: La Traversa: 900 m: 3 VII 1915: Querci [leg.]—Reiss & Tremewan (1967): *Zygaena lonicerae hertae brevicornibus* (ab.).

britanniae (ra)—[*Zygaena lonicerae*] 'subspecies' *lonicerae* 'race' *britanniae* Verity, 1925—Entomologist's Rec. J. Var. 37:117, pl. 8, figs. 56, 57—Syntypes 9 males, 6 females [Great Britain]: Yorks[hire]: Warthill: VII 1921: Smith [leg.]—Reiss & Tremewan (1967): Junior subjective synonym of *Zygaena lonicerae transferens* Verity, 1925; misspelled 'brittaniae'.

caerulea (if)—*Procris cognata* 'forma' *caerulea* Verity, 1946—Redia 31(1945/46):148—Syntype 1 male [N. Italy]: Lago Maggiore: Intra: Pian Quaggie: 950 m: 7 VI 1922: Verity [leg.].

caerulea (if)—*Procris cognata* 'forma' *caerulea* Verity, 1946—Redia

31(1945/46):134—Holotype male Italia centrale: Toscana: [Firenze]: Fiesole: Monte Fanna: 15 VII 1917: Querci [leg.].

caerulea (if)—*Adscita mannii* 'razza' *bellieri* 'forma' *caerulea* Verity, 1946—Redia 31(1945/46):143—Syntype 1 female [S. Italy]: Isola di Sicilia: Palermo: Monreale: S. Martino: 900 m: 5 V 1918: Querci [leg.].

caerulaeochsenheimeri (ra)—*Zygaena filipendulae* 'eserge' *stoechadis* 'razza' *caeruleochsenheimeri* Verity, 1930—Memorie Soc. ent. ital. 9:23—Syntypes 35 males, 28 females [N. Italy]: Alpi Pennine: Vanzone: 700 m: 10-17 VII 1924, 16 VII-4 VIII 1928: Verity [leg.]—Reiss & Tremewan (1967): *Zygaena filipendulae caeruleochsenheimeri* [nec Verity] (ssp.).

*calabra (ra)—*Zygaena filipendulae* 'race' *calabra* Verity, 1917—Bull. Soc. ent. Fr. 1917:223—Syntypes 5 males, 3 females Italia meriodionale: Calabria: Aspromonte: 1200 m: 14-21 VII 1914: Querci [leg.]—Reiss & Tremewan (1967): *Zygaena filipendulae calabra* (ssp.).

calabraochsenheimeri (ra)—*Zygaena filipendulae* 'subspecies' *stoechadis* 'race' *calabraochsenheimeri* Verity, 1921—Entomologist's Rec. J. Var. 33:112—Syntypes 6 males, 5 females [S. Italy]: Catena: Costera calabra: Cosenza: S. Fili: 900 m: 20 V-27VI 1920: Querci [leg.]—Name originally proposed hyphenated: *calabra-ochsenheimeri.*—Reiss & Tremewan (1967): *Zygaena filipendulae calabraochsenheimeri* [nec Verity] (ssp.).

calabricola (nn)—*Anthrocera (Argumenia) carniolica* 'razza' *calabricola* Verity, 1946—Redia 31(1945/46):67—Replacement name for unavailable infrasubspecific name *Zygaena carniolica apennina calabrica* Turati, 1913, said to be preoccupied by available name *Zygaena transalpina calabrica* Calberla, 1895.—Reiss & Tremewan (1967): *Zygaena carniolica calabricola* [nec Verity] (ssp.).

CALEDONIAE (ex)—*Zygaena fulvia* 'eserge' *caledoniae* Verity, 1930— Memorie Soc. ent. ital. 9:21—Holotype 1 female [Great Britain]: Sound of Hull: 1 V 1921.—Reiss & Tremewan (1967): Junior subjective synonym of *Zygaena loti scotica* Rowland-Brown, 1919.

*carnica (ra)—*Zygaena purpuralis* 'razza' *carnica* Verity, 1930— Memorie Soc. ent. ital. 9:12—Lectotype male (Naumann, 1983) [N. Italy]: Alpi Carniche: Sappada: 1300 m: 15 VII 1925: Verity [leg.]; paralectotypes 16 males, 17 females same data but 9-25 VII 1925.—Reiss & Tremewan (1967) and Naumann (1983): *Zygaena purpuralis carnica* (ssp.).

centralitaliae (if)—[*Zygaena lonicerae*] 'subspecies' *trifolii* 'form' *centralitaliae* Verity, 1925.—Entomologist's Rec. J. Var. 37:117, pl. 8, figs. 63-66.—Syntypes 2 males, 1 female; 1 male, 1 female Italia centrale: Piceno: Massiccio Sibillini: 1500 m: 23 VII 1918, VI 1913; 1 male Italia centrale: Ascoli Piceno: Pizzo Tre Vescovi: 18-24 VII 1923: Querci

[leg.].—Reiss & Tremewan (1967): *Zygaena lonicerae pauper cen-tralitaliae* (ab.).

*cicaleti (ra)—*Zygaena fulvia* 'razza' *cicaleti* Verity, 1930—Memorie Soc. ent. ital. 9:19—Syntypes 118 males, 36 females [Italy: Toscana]: Firenze: Pian di Mugnone: 12 V-13 VI 1915, 1-15 VIII 1915: Quer [leg.].—Reiss & Tremewan (1967): *Zygaena loti cicaleti* (ssp.).

crasseunco (if)—*Zygaena fulvia* 'forma' *crasseunco* Verity, 1930—Memorie Soc. ent. ital. 9:20—Type-locality not known.—Reiss & Tremewan (1967): *Zygaena loti tuscomodica crasseunco* (ab.).

decreta (ra)—[*Zygaena lonicerae*] 'subspecies' *trifolii* 'race' *decreta*, Verity, 1925—Entomologist's Rec. J. Var. 37:117, pl. 8, fig. 34-36—Syntypes 33 males, 22 females [Great Britain]: Sussex: Grosvenor [leg.]—Reiss & Tremewan (1967): *Zygaena trifolii decreta* [nec Verity] (ssp.).

denticulata (if)—*Adscita mannii* 'f[orma]' *denticulata* Verity, 1946—Redia 31(1945/46):140—[Italy]: Genova; Gavinana.

dimorphica (ra)—*Zygaena lonicerae* 'subspecies' *transferens* 'race' *dimorphica* Verity, 1925—Entomologist's Rec. J. Var. 37:117, pl. 8, figs. 54, 55—Syntypes 5 males, 4 females [S. Italy]: Catena Costiera Calabria: Cosenza: San Fili: 1-23 VI 1920: Querci [leg.]—Reiss & Tremewan (1967): Junior subjective synonym of *Zygaena lonicerae herthae* Stauder, 1920.

divisa (if)—*Zygaena oxytropis divisa* 'nom.nov.' Verity, 1916—Boll. Soc. ent. ital. 47:77—[Italy: Macerata]—Reiss & Tremewan (1967): *Zygaena oxytropis sibyllina divisa* (ab.).

duponcheli (ra)—*Zygaena filipendulae* 'subspecies' *stoechadis* 'race' *duponcheli* Verity, 1921—Entomologist's Rec. J. Var. 33:124—Syn-types(?) 1 male [France]: Alpes-Mar[itimes]: env. de Nice: 8-10 VIII 1907: Oberthuer [leg.]; 2 males Alpes Maritimes: Vallee de Loup; 1 male Alpes Maritimes: Bar de Loups.—Reiss & Tremewan (1967): *Zygaena filipendulae duponcheli* [nec Verity] (ssp.).

duponcheliella (sf)—[*Zygaena lonicerae*] 'subspecies' *trifolii* 'race' *duponcheliana* '2nd gen.' *duponcheliella* Verity, 1925—Entomologist's Rec. J. Var. 37:117, pl. 8, figs. 44-45—Syntypes 3 males, 1 female [France]: Rognac: Marais 24 IX 1916—Reiss & Tremewan (1967): *Zygaena trifolii dumezi duponcheliella* (f.t.).

elongata (if)—*Zygaena achillae elongata* 'nom.nov.' Verity, 1916—Boll. Soc. ent. ital. 47:73—Italy: Macerata.—Type-material said to be deposited in Oberthuer's collection.—Reiss & Tremewan (1967): *Zygaena loti aspera elongata* (ab.).

EMENDATA [ssp]—*Zygaena transalpina emendata* 'nom.nov.' Verity, 1916—Boll. Soc. ent. ital. 47:76—Italy: Macerata: Colle Torri; type-

material lost—Name originally published in trinominal combination, given the rank of subspecies by implication.—Reiss & Tremewan (1967): *Zygaena transalpina emendata* (ssp.).

*eminens (ra)—*Zygaena (Agrumenia) -carniolica* 'razza' *eminens* Verity, 1946—Redia 31(1945/46):64—Syntypes 15 males, 9 females Italia centrale: Firenze: Firenzuola: 500 m: V-VII 1913-17: Querci & Verity [leg.]; 2 males, 2 females Italia centrale: Firenze: Traversa: 900 m: 4-5 VII 1915: Querci [leg.]; 5 males, 6 females Italia centrale: Toscana: Palazzuolo Romagna; 700 m: 4 VII-19 VIII 1917: Querci [leg.]—Reiss & Tremewan (1967): *Zygaena carniolica eminens* (ssp.).

emirubra (if)—*Zygaena achillae emirubra* 'nom.nov.' Verity, 1916—Boll. Soc. ent. ital. 47:73—Italy: Macerata: Piceno; type-material said to be deposited in Oberthuer's collection.—Treated as an individual form by implication.—Reiss & Tremewan (1967): *Zygaena loti aspera emirubra* (ab.).

erythraeformis (if)—*Zygaena rubicunda erythraeformis* 'n.var.' Verity, 1916—Bull. Soc. ent. Fr. 1916:289—Italy: Sicily: Palermo.—Proposed explicitly for individual form.—Reiss & Tremewan (1967): *Zygaena erythrus saportae erythraeformis* (ab.).

etruriae (ra)—[*Zygaena lonicerae*] 'subspecies' *lonicerae* 'race' *etruriae* Verity, 1925—Entomologist's Rec. J. Var. 37:117, pl. 8, figs. 70-71—Syntypes 5 males, 3 females Italia centrale: Toscana: Monte Senario: 700 m: 12 VII 1918: Verity [leg.]; 2 males, 3 females [Italy: Toscana: Appennino Pistoiese]: Abetone: [1500 m]: 8-10 VII [19]12.—Reiss & Tremewan (1967): *Zygaena lonicerae etruriae* [nec Verity] (ssp.).

etrusca (ra)—*Zygaena filipendulae* 'subspecies' *stoechadis* 'race' *etrusca* Verity, 1921—Entomologist's Rec. J. Var. 33:125—Syntypes 2 males, 3 females Italia centrale: Toscana: Firenzuola: Palasarcio: 150 m; 3 males, 2 females same data but: Cevigliao: 250 m; all specimens 9 VII 1917: Verity [leg.]—Reiss & Tremewan (1967): *Zygaena filipendulae etrusca* [nec Verity] (ssp.).

excelsior (ra)—*Zygaena sarpedon* 'eserge' *punctum* 'razza' *excelsior* Verity, 1930—Memorie Soc. ent. ital. 9:12—Syntypes 41 males, 11 females Italia centrale: Ascoli Piceno: Pizzo Tre Vescovi: 10-20 VII 1923: Querci [leg.]—Reiss &Tremewan (1967): *Zygaena punctum excelsior* [nec Verity] (ssp.).

*florentina (ra)—*Zygaena carniolica* 'razza' *florentina* Verity, 1920—Boll. Lab. Zool. gen. agr. R. Scuola Agric. Portici 14:41—Syntypes 34 males, 12 females Italia centrale: Firenze: Pian di Mugnone.—Reiss & Tremewan (1967): *Zygaena carniolica florentina* (ssp.).

frigidochsenheimeri (ra)—*Zygaena filipendulae* 'eserge' *stoechadis* 'razza' *frigidochsenheimeri* Verity, 1930—Memorie Soc. ent. ital. 9:23—Syntypes 52 males, 42 females [N. Italy]: Alpi Carniche: Sappada: 1200

m: 9-31 VII 1926—Verity [leg.]; 17 VI-21 VII 1915/16: Querci [leg.]—Reiss
& Tremewan (1967): *Zygaena filipendulae frigidochsenheimeri* [nec
Verity] (ssp.).

glaciei (ra)—[*Zygaena lonicerae*] 'subspecies' *lonicerae* 'race' *glaciei*
Verity, 1925—Entomologist's Rec. J. Var. 37:117, pl. 8, fig. 86—Syntypes
1 male, 1 female [N. Italy: Piemonte]: Alpi Pennine: [Val] Formazza:
1300 m: 4 VIII 1924.—Reiss & Tremewan (1967): *Zygaena lonicerae*
glaciei [nec Verity] (ssp.).

*glacieimagismaculata (ra)—*Zygaena lonicerae* 'razza' *glacieimagis-*
maculata Verity, 1930—Memorie Soc. ent. ital. 9:25—Syntypes 31
males, 36 females [N. Italy]: Alpi Carniche: Sappada: 1300 m: 4 VII-7
VIII 1926: Verity [leg.].—Reiss & Tremewan (1967): *Zygaena lonicerae*
glacieimagismaculata (ssp.).

*glauca (ra)—*Adscita mannii* 'razza' *glauca* Verity, 1946—Redia
31(1945/46):144—Syntypes 4 males, 1 female [C. Italy: Toscana]: Appen-
nino Pistoiese: Abetone: 1000 m: 10-25 VII 1929, 9 VII 1912.

*gracilis (ra)—*Adscita mannii* 'razza' *gracilis* Verity, 1946—Redia
31(1945/46):144—Syntypes 8 males, 4 females [C. Italy]: Abruzzi: Gran
Sasso: [sopra Castel del Monte]: 1300-1500 m: 1939: Romei [leg.].

grosvenori (hy)—[*Zygaena lonicerae*] 'subspecies' *trifolii* 'hybrid *dec-*
reta x *tutti*' *grosvenori* Verity, 1925—Entomologist's Rec. J. Var. 37:117,
pl. 8, fig. 39—Syntypes 2 males [Great Britain]: Sussex: 25 VII 1921:
Grosvenor [leg.].—Reiss 7 Tremewan (1967): *Zygaena trifolii* 'hybrid'
grosvenori (unavailable name).

gueneeiformis (if)—*Zygaena oxytropis guenneiformis* 'nom.nov.'
Verity, 1916—Bull. Soc. ent. Fr. 1916:78—Italy: Macerata (by implica-
tion).—Treated as an individual form by implication.—Reiss & Tremewan
(1967): *Zygaena oxytropis sibyllina gueneeiformis* (ab.).

guttata (if)—*Zygaena filipendulae* 'form' *guttata* Verity, 1921—Ento-
mologist's Rec. J. Var. 33:149—Type-locality not known.—Reiss &
Tremewan (1967): *Zygaena filipendulae aterrima guttata* (ab.).

hibera (ra)—[*Zygaena lonicerae*] 'subspecies' *palustris* 'race' *hibera*
Verity, 1925—Entomologist's Rec. J. Var. 37:117, pl. 8, figs. 1, 2—
Syntypes 7 males, 3 females Espana: [ovideo]: Asturias: 20 VII 1920—
Reiss & Tremewan (1967): *Zygaena trifolii hibera* [nec Verity] (ssp.).

hibernuncula (if)—[*Zygaena lonicerae*] 'subspecies' *palustris* 'race'
hibera 'form' *hibernuncula* Verity, 1925—Entomologist's Rec. J. Var.
37:117, pl. 8, figs. 3-5—Syntypes 5 males, 3 females Espana: [Ovideo]:
Asturias: 20 VII [19]20.—Reiss & Tremewan (1967): *Zygaena trifolii*
hibera hibernuncula (ab.).

hispana (ra)—*Zygaena loti* 'subspecies' *transalpina* 'race' *hispana*
Verity, 1920—Entomologist's Rec. J. Var. 32:31—Spain: Valenzia (=

Valencia); holotype said to be deposited in the Ruehl's collection.—Reiss
& Tremewan (1967): Junior subjective synonym of *Zygaena transalpina
calabrica* [sic] Calberla, 1895.

*hyalicolor (ra)—*Adscita alpina* 'razza' *hyalicolor* Verity, 1946—Redia
31(1945/46):150—Syntypes 3 males, 1 female [N. Italy]: Alpi Carniche:
Sappada: [1300 m]: 22 VII [19]36; same data but: Fenili d'Olbe: 1600 m: 5
VII 1936; [all Rocca leg.].

incisa (if)—*Zygaena purpuralis* 'race' *normanna* 'form' *incisa* Verity,
1922—Entomologist's Rec. J. Var. 34:34—Syntype 1 female [N. France]:
Eure: Porta de l'Arche: 5 VIII 1916—The specimen was designated lec-
totype of *Z. purpuralis normanna* Verity, 1922, by Naumann (1983).—
Reiss & Tremewan (1967): *Zygaena diaphana normanna incisa* (ab.).

intermixta (ra)—*Zygaena lonicerae* 'subspecies' *transferens* 'race'
intermixta Verity, 1920—Entomologist's Rec. J. Var. 32:76—Syntypes
23 males, 26 females [Spain]: Aragon: Orihuela: 1700 m: 7-13 VII [19]24;
1 male Aragon: Noguera: 1400 m: 8 VII [19]24; all: Querci [leg.]—Reiss &
Tremewan (1967): *Zygaena lonicerae intermixta* [nec Verity] (ssp.).

intricata (sf)—*Zygaena lonicerae* 'subspecies' *trifolii* 'race' *syracusia*
'seasonal form' *intricata* Verity, 1926—Entomologist's Rec. J. Var.
38:23—Syntypes 7 males, 34 females [Spain]: Catalonia: Llobregat: 2 m:
2-9 X 1925: Querci [leg.]—Reiss & Tremewan (1967): *Zygaena trifolii
barcelonensis intricata* (f.t.).

*isarca (ra)—*Zygaena purpuralis* 'race' *isarca* Verity, 1922—Ento-
mologist's Rec. J. Var. 34:32—Lectotype male (Naumann, 1983): [N.
Italy]: Suedtirol: 191[?]; paralectotypes 5 males, 4 females: same data.—
Reiss & Tremewan (1967): *Zygaena purpuralis isarca* (ssp.).

italaparva (ra)—*Zygaena sarpedon* 'eserge' *punctum* 'razza' *italaparva*
Verity, 1930—Memorie Soc. ent. ital. 9:14—Syntypes 12 males, 9 females
[C. Italy]: Toscana: Firenze: Pian di Mugnone: 1-29 VII 1916; Colline di
Firenze: 200 m: 20-22 VII 1914, 3-6 VII 1921: Querci [leg.]—Reiss &
Tremewan (1967): *Zygaena punctum italaparva* [nec Verity] (ssp.).

*jurae (ra)—*Zygaena purpuralis* 'race' *jurae* Verity, 1922—Ento-
mologist's Rec. J. Var. 34:34—Lectotype male (Naumann, 1983): Jura
Suisse: 9 VII [19]20; paralectotypes 15 males, 14 females: same data.—
Reiss & Tremewan (1967): *Zygaena purpuralis jurae* (ssp.).

latelimbata (if)—*Zygaena filipendulae* 'form' *latelimbata* Verity,
1921—Entomologist's Rec. J. Var. 33:147—Type-locality not stated.—
Reiss & Tremewan (1967): *Zygaena filipendulae major latelimbata*
(ab.).

laterubra (ra)—*Zygaena rhadamanthus* 'subspecies' *oxytropis* 'race'
laterubra Verity, 1920—Entomologist's Rec. J. Var. 32:160—Syntypes 2
males, 9 females Suditalia: Massiccio delle Mainarde: Valle Mollarino:

[Villagrande, Villalatina]: 500 m: 18 VI 1919: Querci [leg.].—Reiss & Tremewan (1967): *Zygaena oxytropis laterubra* [nec Verity] (ssp.).

latina (ra)—*Zygaena loti* 'subspecies' *transalpina* 'race' *latina* Verity, 1920—Entomologist's Rec. J. Var. 32:31—Syntypes 21 males [S. Italy: Campania]: Caserta: Atina, V[illa] Latina: 3-16 VII 1919: Rocci [leg.].— Reiss & Tremewan (1967): *Zygaena transalpina latina* [nec Verity] (ssp.).

latiorelimbata (if)—*Zygaena filipendulae* 'form' *latiorelimbata* Verity, 1921—Entomologist's Rec. J. Var. 33:147—Type-locality not known.— *Zygaena filipendulae etrusca latiorelimbata* (ab.).

latissimelimbata (if)—*Zygaena filipendulae* 'form' *latissimelimbata* Verity, 1921—Entomologist's Rec. J. Var. 33:147—Type-locality not known.—Reiss & Tremewan (1967): *Zygaena filipendulae aterrima latissimelimbata* (ab.).

*****ligus** (ra)—*Anthrocera (Polymorpha) ephialtes* 'razza' *ligus* Verity, 1946—Redia 31(1945/46):78—Syntypes 4 males [NW Italy: Savona]: Celle Lig[ure]: VI 1914—Reiss & Tremewan (1967): *Zygaena ephialtes ligus* (ssp.).

longicornibus (if)—[*Zygaena lonicerae*] 'subspecies' *trifolii* 'race' *decreta* 'form' *longicornibus* Verity, 1925—Entomologist's Rec. J. Var. 37:117, pl. 8, figs. 40, 41.—Great Britain: Sussex: Grosvenor leg.—Reiss & Tremewan (1967): *Zygaena trifolii decreta longicornibus* (ab.).

loniceraeformis (if)—*Zygaena stoechadis dubia loniceraeformis* Verity, 1916—Boll. Soc. ent. ital. 47:74—Type-locality not known.—Reiss & Tremewan (1967): *Zygaena filipendulae etrusca lonicraeformis* (ab.).

*****lusitaniaemixta** (ra)—*Zygaena lonicerae* 'razza' *lusitaniaemixta* Verity, 1930—Memorie Soc. ent. ital. 9:25—Syntypes 66 males, 39 females Portugal: Serra da Estrella: 1800 m: 13 VI-23 VII 1927: Querci [leg.].—Reiss & Tremewan (1967): *Zygaena trifolii lusitaniaemixta* (ssp.).

macula (if)—*Zygaena filipendulae* 'form' *macula* Verity, 1921— Entomologist's Rec. J. Var. 33:147—Type-locality not known.—Reiss & Tremewan (1967): *Zygaena filipendulae aterrima macula* (ab.).

magismaculata (ra)—[*Zygaena lonicerae*] 'subspecies' *lonicerae* 'race' *magismaculata* Verity, 1925—Entomologist's Rec. J. Var. 37:117, pl. 8, figs. 78, 79—Syntypes 5 males, 9 females Suisse: Geneve: 25 V, 10, 24, 29 VI, 8, 14, 29 VII, 1915-1923: Weber and Bolle [leg.].—Reiss & Tremewan (1967): *Zygaena lonicerae magismaculata* [nec Verity] (ssp.).

*****magnalpina** (ra)—*Zygaena purpuralis* 'race' *magnalpina* Verity, 1922—Entomologist's Rec. J. Var. 34:33—Lectotype male (Naumann, 1983) [France: Hautes-Pyrenees]: Gedre: Rondou [leg.]; paralectotypes 8 males, 1 female same data.—Reiss & Tremewan (1967): *Zygaena pur-*

puralis magnalpina (ssp.); Naumann (1983): *Zygaena purpuralis magnalpina* (ssp.).

magnamacula (if)—*Zygaena filipendulae* 'form' *magnamacula* Verity, 1921—Entomologist's Rec. J. Var. 33:148—Type-locality not stated or known.—Reiss & Tremewan (1967): *Zygaena filipendulae aterrima magnamacula* (ab.).

magnaustralis (ra)—[*Zygaena lonicerae*] 'subspecies' *trifolii* 'race' *magnaustralis* Verity, 1925—Entomologist's Rec. J. Var. 37:117—Holotype male Algerie: Faroult [leg.]: ex Turati coll.—Reiss & Tremewan (1967): *Zygaena trifolii magnaustralis* [nec Verity] (ssp.).

*****magnaustralis** (ra)—*Anthrocera (Agrumenia) carniolica* 'razza' *magnaustralis* Verity, 1946—Redia 31(1945/46):66—Syntypes 8 males, 5 females [C. Italy: Lazio: Roma]: Formia: 21 VI 1938: Querci [leg.].—Reiss & Tremewan (1964) erroneously considered this name to be junior secondary homonym of *Zygaena lonicerae trifolii magnaustralis* Verity, 1925, which is unavailable on account of its quadrinominal original combination, and were therefore unjustified to replace it with *Zygaena carniolica formiacola* Reiss & Tremewan, 1964.—Reiss & Tremewan (1967): *Zygaena carniolica formiacola*—the above error repeated.

microchsenheimeri (ra)—*Zygaena filipendulae* 'subspecies' *stoechadis* 'race' *microchsenheimeri* Verity, 1921—Entomologist's Rec. J. Var. 33:114—Syntypes 37 males, 9 females Sud Italia: Massiccio delle Mainarde: Valle Mollarino: 10-18 VII 1919: Querci [leg.].—Reiss & Tremewan (1967): *Zygaena filipendulae microchsenheimeri* [nec Verity] (ssp.).

microduponcheli (sf)—*Anthrocera (Anthrocera = Thermophila) filipendulae* 'razza' *duponcheli* '2nd gen.' *microduponcheli* Verity, 1946—Redia 31(1945/46):67—Syntypes 6 males, 14 females [S. France]: A[lpes]-M[aritimes]: Venice: 21 VIII - 2 IX 1937: Verity [leg.].—Reiss & Tremewan (1967): *Zygaena filipendulae duponcheli microduponcheli* (f.t.).

microdysrepta (ra)—*Zygaena sarpedon* 'eserge' *punctum* 'razza' *microdysrepta* Verity, 1930—Memorie Soc. ent. ital. 9:13—Syntypes 3 males, 1 female Italia centrale: Caserta: Monti Aurunci: Valle del Petrella: 1200 m: 30 VI 1911.—Reiss & Tremewan (1967): *Zygaena punctum faitensis microdysrepta* (f.loc.).

microetrusca (sr, sf)—*Anthrocera (Anthrocera = Thermophila) filipendulae* 'razza' *etrusca* 'sottorazza' *microetrusca* Verity, 1946—Redia 31(1945/46):68—Syntypes 12 males, 6 females [C. Italy: Toscana: Chianti]: Greve: S. Giusto: 22 VII - 1 VIII 1931: Rocci [leg.].—Reiss & Tremewan (1967): *Zygaena filipendulae etrusca microetrusca* (f.t.).

microhydesari (sr)—*Anthrocera (Agrumenia) carniolica* 'razza' *hydesari* 'sottorazza' *microhydesari* Verity, 1946—Redia 31(1945/46):61—

Syntypes 15 males, 5 females [N. Italy: Torino]: Monte Musime: 27 VII 1930: Rocci [leg.].—Reiss & Tremewan (1967): Junior subjective synonym of *Zygaena carniolica notissima* Rocci, 1941.

*microseeboldi (ra)—*Anthrocera (Anthrocera = Thermophila) filipendulae* 'razza' *microseeboldi* Verity, 1946—Redia 31(1945/46):68—Syntypes 3 males, 7 females [NW Spain]: Asturias: Pajares: 1300 m: 6-8 VIII 1924: Romei [leg.].—Reiss & Tremewan (1967) Junior subjective synonym of *Zygaena filipendulae kricheldorffiana* Reiss, 1936.

minuens (sr)—[*Zygaena lonicerae*] 'subspecies' *lonicerae* 'race' *lonicerae* 'secondary race' *minuens* Verity, 1925—Entomologist's Rec. J. Var. 37:117, pl. 8, figs. 82, 83—Syntypes 5 males, 4 females [Germany: Bavaria]: Gammersdorf, Brandelberg: 17-29 VII 1923.—Reiss & Tremewan (1967): *Zygaena lonicerae minuens* [nec Verity] (ssp.).

minuscola (sr)—*Adscita alpina* 'razza' *hyalicolor* 'sottorazza' *minuscola* Verity, 1946—Redia 31(1945/46):151—Syntypes 1 male [N. Italy]: Val di Gares: Porta di Ferrade: 1000 m; 1 male, 1 female [N. Italy]: C[olle] di Campione: 1182 m: 28 VI 1937: Rocca [leg.].

minutissima (nn)—*Zygaena lonicerae* 'subspecies' *lonicerae* 'race' *lonicerae* 'form' *minutissima* Verity, 1926—Entomologist's Rec. J. Var. 38:73—Replacement name for *Zygaena lonicerae minor* Tutt, 1899, said to be preoccupied by *Zygaena trifolii minor* Tutt, 1899.—Reiss & Tremewan (1967): *Zygaena lonicerae transferens minutissima* (ab.).

*mirabilis (ra)—*Zygaena purpuralis* 'race' *mirabilis* Verity, 1922—Entomologist's Rec. J. Var. 34:32—Lectotype female (Naumann, 1983) [S. Italy]: Catena: Costiera Calabria: Cosenza: San Fili: 4 VI 1926: Querci [leg.]; paralectotypes 4 males, 9 females.—The above cited designation of the lectotypes is invalid because the specimen selected does not belong to the type-series: it was collected as late as 1926 while the taxon was already named in 1922.—Reiss & Tremewan (1967): *Zygaena purpuralis mirabilis* (ssp.); Naumann (1983): *Zygaena purpuralis mirabilis* (ssp.).

misera (ra)—[*Zygaena lonicerae*] 'subspecies' *lonicerae* 'race' *misera* Verity, 1925—Entomologist's Rec. J. Var. 37:117, pl. 8, figs. 84, 85—Syntypes 2 males [Great Britain]: Sussex: Grosvenor [leg.].—Reiss & Tremewan (1967): Junior subjective synonym of *Zygaena lonicerae transferens* Verity, 1926.

*miserrima (ra)—*Zygaena erythrus* 'race' *miserrima* Verity, 1931—Entomologist's Rec. J. Var. 34:31—Syntype 1 female [N. Italy]: Piemonte: Musime: coll. Granelli (ex Oberthuer).—Reiss & Tremewan (1967): *Zygaena erythrus miserrima* (ssp.).

*modesta (ra)—*Procris subsolana* 'razza' *modesta* Verity, 1946—Redia 31(1945/46):129—Syntypes 5 males [C. Italy]: Abruzzi: Gran Sasso: 1300-1500 m: 1939: Romei [leg.].

montivaga (if)—*Zygaena stoechadis dubia montivaga* 'nom.nov.' Verity, 1916—Boll. Soc. ent. ital. 47:73—Syntypes 20 males, 7 females Italia centrale: Piceno: Monti Sibillini: 1200 m: VII 1913; 5 males, 4 females same data but: Bolognola: 1500 m: 19-26 VII 1913: Querci [leg.].—Reiss & Tremewan (1967): *Zygaena filipendulae montivaga* [nec Verity] (ssp.).

***nantuatium** (ra)—*Anthrocera (Polymorpha) transalpina* 'razza' *nantuatium* Verity, 1946—Redia 31(1945/46):76—Syntypes 14 males, 11 females [Switzerland]: Vaud: Bex, Lavey: 1-20 VII 1932.—Reiss & Tremewan (1967): *Zygaena transalpina nantuatium* (ssp.).

***normanna** (ra)—*Zygaena purpuralis* 'race' *normanna* Verity, 1922—Entomologist's Rec. J. Var. 34:34—Lectotype male (Naumann, 1983) [France]: Eure: Pont del'Arche: 18 VII 1905; paralectotypes 6 males, 5 females—Reiss & Tremewan (1967): *Zygaena diaphana normanna* (ssp.); Naumann (1983): *Zygaena minos normanna* (ssp.).

oblongomacula (if)—*Zygaena filipendulae* 'eserge' *stoechadis* 'razza' *frigidochsenheimeri* 'forma' *oblongomacula* Verity, 1930—Memorie Soc. ent. ital. 9:24—Holotype (?) male [N. Italy]: Alpi Sappada: 1300 m: 29 VII 1926: Verity [leg.].—Reiss & Tremewan (1967): *Zygaena filipendulae frigidochsenheimeri ablongomacula* (ab.).

oraria (ra)—*Zygaena filipendulae* 'subspecies' *stoechadis* 'race' *oraria* Verity, 1921—Entomologist's Rec. J. Var. 33:126—Syntypes 28 males, 18 females [C. Italy]: Lucca: Forte dei Marmi: 18 VII-8VIII 1918.—Reiss & Tremewan (1967): *Zygaena filipendulae oraria* [nec Verity] (ssp.).

oxytropiferens (ra)—*Zygaena radamanthus* 'subspecies' *rhadamanthus* race' *oxytropiferens* Verity, 1920—Entomologist's Rec. J. Var. 32:161—S. France: Alpes Maritimes: Menton: 1907; name for specimens figured by Oberthür (1910) in Etud. Lepid. comp. 4:592.—Reiss & Tremewan (1967): *Zygaena rhadamnathus oxytropiferens* [nec Verity] (ssp.).

palustrella (ra)—[*Zygaena lonicerae*] 'subspecies' *palustris* 'race' *palustrella* Verity, 1925—Entomologist's Rec. J. Var. 37:117, pl. 8, figs. 8, 9—Syntypes 3 males, 3 females [Great Britain]: Surrey: 5-7 VI 1922: Grosvenor [leg.].—Reiss & Tremewan (1967): *Zygaena trifolii palustrella* [nec Verity] (ssp.).

paraustralis (ra)—*Zygaena lonicerae* 'subspecies' *trinacria* 'race' *paraustralis* Verity, 1926—Entomologist's Rec. J. Var. 38:11, 24—Syntypes 2 males [S. Italy]: Sicilia: Rag[usa leg.].—Reiss & Tremewan (1967): Junior subjective synonym of *Zygaena trifolii syracusia* Zeller, 1847.

***parvalpina** (ra)—*Zygaena purpuralis* 'race' *parvalpina* Verity, 1922—Entomologist's Rec. J. Var. 34:33—Lectotype male (Naumann, 1983) [N. Italy: Alpi Marittime]: Valdieri: 1909; paralectotypes 4 males, 2 females same locality but: 3 VII [19]10, 25 VII [19]11. One female paralectotype

(i.e. one of the former syntypes) belongs to a different species, known under well established name *Zygaena brizae vesubiana* Le Charles, 1933; since the designation by Naumann (1983) of the name bearing lectotype, this fact is of no consequence so far as the nomenclature of any of these two species is concerned.—Reiss & Tremewan (1967): *Zygaena purpuralis parvalpina* (ssp.); Naumann (1983): *Zygaena purpuralis parvalpina* (ssp.).

paulula (ra)—*Zygaena filipendulae* 'subspecies' *filipendulae* 'race' *paulula* Verity, 1921—Entomologist's Rec. J. Var. 33:89—Syntypes 1 male, 1 female [N. Italy]: Suedtirol: [Solfer-Joch]: 191[?].—Reiss & Tremewan (1967): *Zygaena filipendulae paulula* [nec Verity] (ssp.).

pauper (ra)—[*Zyganea lonicerae*] 'subspecies' *lonicerae* 'race' *pauper* Verity, 1925—Entomologist's Rec. J. Var. 37:117, pl. 8, figs. 61. 62—Syntypes 1 male, 1 female Italia centrale: Piceno: Monti Sibillini: 1800 m; 1 male, 2 females same data but: Pizzo Tre Vescovi: 1700-1800 m: 26 VII 1923; Italia centrale: Marche: Alta Valle di Fergano: 1400 m: 2 VII 1920; 1 male same date but: Massacci di Bolognola: 1200 m: 7 VII 1922; [mostly] Querci [leg.].—Reiss & Tremewan (1967): *Zygaena lonicerae pauper* [nec Verity] (ssp.).

paupercula (sr)—*Zygaena filipendulae* 'subspecies' *filipendulae* 'race' *pulchrior* 'subrace' *paupercula* Verity, 1921—Entomologist's Rec. J. Var. 33:90—Syntypes 2 males, 1 female [Austria: Wien]: Gumpoldskirchen, Oberweiden: VI, 12 VI 1916.—Reiss & Tremewan (1967): Junior subjective synonym of *Zygaena filipendulae pulchrior* [nec Verity].

pauperetincta (ra)—[*Zygaena lonicerae*] 'subspecies' *lonicerae* 'race' *pauperetincta* Verity, 1925—Entomologist's Rec. J. Var. 37:117, pl. 8, figs. 68, 69—Syntypes 2 males Italia centrale: Marche: Valle del'Fergano: 1400 m: 2 & 19 VII 1922; 1 male Italia centrale: Ascoli Piceno: Valle del Frostrone: 1000 m: 23 VIII 1922; 5 males, 7 females Italia centrale: Ascoli Piceno: Pizzo Tre Vescovi: 1200 m: 18-30 VII 1923; 9 males, 3 females Italia centrale: Macerata: Monti Sibillini: Bolognola: Massacci di Bolognola: 1200-1600 m: 16 VI 1918, 23 VI 1922, 6-23 VII 1923; [mostly] Querci [leg.].—Reiss & Tremewan (1967): *Zygaena lonicerae pauperetincta* [nec Verity] (ssp.).

plutonia (if)—*Zygaena purpuralis minos* 'form' *plutonia* Verity, 1922—Entomologist's Rec. J. Var. 34:34—Holotype male [Austria: Wien]: Werger: 1906; described from a single specimen.—Reiss & Tremewan (1967): *Zygaena purpuralis monos plutonia* (ab.).

polygalaeformis (if)—*Zygaena rubicundus polygalaeformis* 'nom.nov.' Verity, 1916—Boll. Soc. ent. ital. 47:71—C. Italy: Macerata: Piano Astore; holotype said to be in the Oberthür collection.—Treated as individual form by implication.—Reiss & Tremewan (1967): *Zygaena*

rubicundus rubicundus polygalaeformis (ab.).

posticeobscurata (if)—*Zygaena lonicerae* 'razza' *vivax* 'forma' *posticeobscurata* Verity, 1920—Boll. Lab. Zool. gen. agr. R. Scuola Agric. Portici 14:39—Syntype 1 male Suditalia: Massiccio delle Mainarde: Valle Mollarino: 500 m: 26 VI 1919: Querci [leg.].—Reiss & Tremewan (1967): *Zygaena lonicerae vivax posticeobscurata* [sic] (ssp.).

*****praeochsenheimeri** (ra)—*Zygaena filipendulae* 'race' *praeochsenheimeri* Verity, 1939—Entomologist's Rec. J. Var. (Suppl.) 51(1):(19)—Syntypes 45 males, 13 females [Greece]: Macedonia: Olympus: [Skala; S. Dionisio]: 900-2500 ft.: VI-VII 1936: Romei [leg.].—Reiss & Tremewan (1967): *Zygaena filipendulae praeochsenheimeri* (ssp.).

*****pseudostatices** (ra)—*Adscita mannii* 'razza' *pseudostatices* Verity, 1946—Redia 31(1945/46):146—Syntypes 1 male, 1 female [S. France]: Alpes Maritimes: Vallee des Loup; 4 males, 1 female A[lpes-] M[aritimes]: St. Barnabe: 21-29 V 1933: Gazel [leg.].

pulcherrima (ra)—*Zygaena filipendulae* 'subspecies' *filipendulae* 'race' *pulcherrima* Verity, 1921—Entomologist's Rec. J. Var. 33:90—Syntypes 32 males, 13 females [France]: Charente Inferieure: Dompierre: 10-18 VI 1908—Boule [leg.].—Reiss & Tremewan (1967): *Zygaena filipendulae pulcherrima* [nec Verity] (ssp.).

pulcherrimaeformis (if)—*Zygaena filipendulae* 'subspecies' *stoechadis* 'form' *pulcherrimaeformis* Verity, 1921—Entomologist's Rec. J. Var. 33:110—Type-locality not known.—Reiss & Tremewan (1967): *Zygaena filipendulae calabra pulcherrima* (ab.).

pulcherrimastoechadis (ra)—*Zygaena filipendulae* 'subspecies' *filipendulae* or *stoechadis* 'race' *pulcherrimastoechadis* Verity, 1921—Entomologist's Rec. J. Var. 33:109—Syntypes 3 males, 11 females Italia settentrionale: Emilia: VI 1917: Costantini [leg.]; 9 males, 4 females same data but: Borzeno: 8-9 VII 1914; 2 males, 1 female same data but: Modena: Colli di Scandiano: 10-13 VII 1914: Respigone [leg.].—Reiss & Tremewan (1967): *Zygaena filipendulae pulcherrimastoechadis* [nec Verity] (ssp.).

pulchrior (ra)—*Zygaena filipendulae* 'subspecies' *filipendulae* or *stoechadis* 'race' *pulchrior* Verity, 1921—Entomologist's Rec. J. Var. 33:90—Syntypes 4 males, 3 females Austria inferior: Klosterneuberg: 9 VII 1916: Höfer [leg.].—Reiss & Tremewan (1967): *Zygaena filipendulae pulchrior* [nec Verity] (ssp.).

pumila (ra)—*Zygaena rhadamanthus* 'subspecies' *oxytropis* 'race' *pumila* Verity, 1920—Entomologist's Rec. J. Var. 32:160—Italy: Toscana: Traversa: Futa Pass: 2700 ft. (= 850 m).—Reiss & Tremewan (1967): *Zygaena oxytropis pumila* [nec Verity] (ssp.).

punctonotata (if)—*Zygaena lonicerae* 'subspecies' *trinacria* 'form'

punctonotata Verity, 1926—Entomologist's Rec. J. Var. 38:12—S. Italy:
Sicily: Palermo: Lupo; type-material said to be deposited in the
Rothschild collection.—Reiss & Tremewan (1967): *Zygaena trilofii
trinacria punctonotata* (ab.).

pyrenaea (ra)—*Zygaena rhadamanthus* 'subspecies' *rhadamanthus*
'race' *pyrenaea* Verity, 1920—Entomologist's Rec. J. Var. 32:161—
Syntypes(?) 7 males S. France: Pyrenees Orientales: [La Trancada
d']Ambuilles: 10 IV 1917; name for specimens described by Oberthür
(1910) in Etud. Lepid. comp. 4:590.—Reiss & Tremewan (1967): *Zygaena
rhadamanthus pyrenaea* [nec Verity] (ssp.).

pyrenes (ra)—*Zygaena filipendulae* 'subspecies' *stoechadis* 'race'
pyrenes Verity, 1921—Entomologist's Rec. J. Var. 33:122—Syntypes 9
males [S. France]: Pyrenees Orientales: Vernet-les-Bains: VIII-IX 1909:
R. Oberthür & Powell [leg.].—Reiss & Tremewan (1967): *Zygaena
filipendulae pyrenes* [nec Verity] (ssp.).

quercii (ra)—*Zygaena rhadamanthus* 'subspecies' *oxytropis* 'race' *quer-
cii* Verity, 1920—Entomologist's Rec. J. Var. 32:160—Syntypes 28 males,
6 females [S. Italy]: Isola di Sicilia: Palermo: Monreale: S. Martino: 800
m: 18-22 V 1918: Querci [leg.].—Reiss & Tremewan (1967): *Zygaena
oxytropis quercii* [nec Verity] (ssp.).

radiis (if)—*Zygaena filipendulae* 'form' *radiis* Verity, 1921—Entomolo-
gist's Rec. J. Var. 33:148—Type-locality not known.—Reiss & Tremewan
(1967): *Zygaena filipendulae aterrima radiis* (ab.).

radiiszonata (if)—*Zygaena filipendulae* 'form' *radiiszonata* Verity,
1921—Entomologist's Rec. J. Var. 33:148—Type-locality not known;
name originally published hyphenated.—Reiss & Tremewan (1967):
Zygaena filipenduale aterrima radiiszonata (ab.).

*roccii (ra)—*Zygaena carniolica* 'razza' *roccii* Verity, 1920—Boll. Lab.
Zool. gen. agr. R. Scuola Agric. Portici 14:42—Syntypes 24 males, 3
females Italia settentrionale: Liguria: Genova: Quezzi: 12 V-2 VI 1917,
1919: Rocci [leg.].—Reiss & Tremewan (1967): *Zygaena carniolica
roccii* (ssp.).

rosella (if)—*Zygaena lonicerae* 'subspecies' *trifolii* 'race' *magnaustralis*
'form' *rosella* Verity, 1926—Entomologist's Rec. J. Var. 38:24—Holotype
male [Spain]: Arragonien.—Reiss & Tremewan (1967): *Zygaena trifolii
noguerensis rosella* (ab.).

rubens (ra)—*Zygaena ephialtes* 'sottospecies' *ephialtes* 'razza' *rubens*
Verity, 1920—Boll. Lab. Zool. gen. agr. R. Scuola Agric. Portici 14:39—
Syntypes 3 males, 1 female [France]: Parigi: Issy, Lardy, Bouray: 27 VII
1919, 15 VII 1920(?).—It is not quite certain whether the specimen col-
lected 15 VII 1920 really belongs to the type-series. Type-locality was
established by Verity (1946) in Redia 31(1945/46):77. Reiss & Tremewan
erroneously rejected the name dated 1920 because of the author's failure

to state the type-locality, considering it nomen nudum, apparently unaware that the stating of type-locality is not a condition for availability of species-group names (cf. International Code of Zoological Nomenclature); they considered the name available as from 1946 (cf. above) and treated it as subspecies: *Zygaena ephialtes rubens* [nec Verity] (ssp.).

*ruberrima (ra)—*Zygaena achillae* 'razza' *ruberrima* Verity, 1920— Boll. Lab. Zool. gen. agr. R. Scuola Agric. Portici 14:37—Syntypes 58 males, 11 females Suditalia: Massiccio delle Mainarde: Valle Mollarino: V-VI 1919: Querci [leg.].—Reiss & Tremewan (1967): *Zygaena loti ruberrima* (ssp.).

rubicundiformis (if)—*Zygaena sarpedon* 'esserge' *punctum* 'razza' *excelsior* 'forma' *rubicundiformis* Verity, 1930—Memorie Soc. ent. ital. 9:13—Syntypes 1 male, 1 femae Italia centrale: Ascoli Piceno: Pizzo Tre Vescovi: 1700 m: 10-15 VII 1928, 18-24 VII 1928: Querci [leg.].—Reiss & Tremewan (1967): *Zygaena punctum excelsior rubicundiformis* (ab.).

rufofimbriata (if)—*Zygaena purpuralis* 'race' *jurae* 'female form' *rufofimbriata* Verity, 1922—Entomologist's Rec. J. Var. 34:35—Syntypes 2 females Suisse: Jura: [Dombresson]—The specimens were also designated paralectotypes of *Zygaena purpuralis jurae* Verity, 1922 (Naumann, 1983); cf. *jurae*.—Reiss & Tremewan (1967): *Zygaena purpuralis jurae rufofimbriata* (ab.).

rubrosuffusa (if)—*Zygaena lonicerae* 'subspecies' *lonicerae* 'form' *rubrosuffusa* Verity, 1926—Entomologist's Rec. J. Var. 38:74—Syntype 1 female [N. Italy]: Valle Anzasca: Vanzone: 1 VIII 1924—Reiss & Tremewan (1967): Junior subjective synonym of *Zygaena lonicerae alpiumgigas incendium* Oberthür, 1909 (ab.).

rubrotecta (if)—*Zygaena purpuralis* 'form' *rubrotecta* Verity, 1922— Entomologist's Rec. J. Var. 34:31—Type-locality not known.—Reiss & Tremewan (1967): *Zygaena purpuralis mirabilis rubrotecta* (ab.).

secundogenita (sf)—[*Zygaena lonicerae*] 'subspecies' *trifolii* 'race' *syracusia* '2nd gen.' *secundogenita* Verity, 1925—Entomologist's Rec. J. Var. 37:117, pl. 8, fig. 23—S. Italy: Sicily: Catania: Plaia; holotype said to be deposited in coll. Turati.—Reiss & Tremewan (1967): *Zygaena trifolii syracusia secundogenita* (ab.).

SIBYLLINA [ssp]—*Zygaena oxytropis sibyllina* 'nom.nov.' Verity, 1916—Boll. Soc. ent. ital. 47:77—Syntypes 53 males, 5 females Italia centrale: Piceno: Monti Sibillini: 1700 m: VI 1913: Querci [leg.]; the name was originally published in trinominal combination without any indication of rank, therefore treated here as subspecies by implication.—Reiss & Tremewan (1967): *Zygaena oxytropis sibyllina* (ssp.).

siciliae (ra)—[*Zygaena lonicerae*] 'subspecies' *trifolii* 'race' *siciliae* Verity, 1925—Entomologist's Rec. J. Var. 37:117, pl. 8, fig. 14—Syntypes 3 males [S. Italy]: Sicilia, Palermo: Rag[usa leg.].—Reiss & Tremewan

(1967): Junior subjective synonym of *Zygaena trifolii syracusia* Zeller, 1847.

*siciliensis (ra)—*Zygaena filipendulae* 'race' *siciliensis* Verity, 1917—Bull. Soc. ent. Fr. 1917:223—Syntypes 5 males, 6 females [S. Italy]: Sicilia: Palermo, Cuccio: Ragusa [leg.].—Reiss & Tremewan (1967): *Zygaena filipendulae siciliensis* (ssp.).

silaecola (nn)—*Zygaena meliloti* 'eserge' *charon* 'razza' *silaecola* Verity, 1930—Memorie Soc. ent. ital. 9:23—Replacement for *Anthrocera meliloti silana* Turati, 1923, said to be a junior secondary homonym of *Zygaena lonicerae silana* Burgeff, 1914, from Calabria, originally treated as 'var.', unmistakeably of subspecific rank by implication.

stricta (if)—*Procris cognata* 'forma' *stricta* Verity, 1946—Redia 31 (1945/46):134—Type-locality not known.

subsyracusia (ra)—[*Zygaena lonicerae*] 'subspecies' *trifolii* 'race' *subsyracusia* Verity, 1925—Entomologist's Rec. J. Var. 37:117, pl. 8, figs. 31-33—Syntypes 2 males, 2 females [France]: St. Pierre Quiberon Pativy: 10-26 VI 1923, 1-13 VI 1924; 5 males, 2 females Plouharnel: Isthame Quiberon: 11 VI-1 VII 1923; 1 male Presqu'ile de Quiberon: V 1928; 1 female Region du Quiberon: 13 VI 1924; 1 female Plouharnel: 16 V 1921.—Reiss & Tremewan (1967): *Zygaena trifolii subsyracusia* [nec Verity] (ssp.).

superdysrepta (ra)—*Zygaena sarpedon* 'eserge' *punctum* 'razza' *superdysrepta* Verity, 1930—Memorie Soc. ent. ital. 9:13—Syntypes (?) 1 male, 5 females [Italy: Latium]: Monti Aurunci: comune di Esperia: path to Madonna delle Grazie; status of specimens uncertain, based upon a group-label in Verity's handwriting: "These 6 specimens that I have from Mr. Stefanelli should be those collected by O. Querci in the Aurunci Mts.: commune di Esperia.—Reiss & Tremewan (1967): *Zygaena punctum faitensis superdysrepta* (f.loc.).

*taurinorum (ra)—*Zygaena cynarae* 'razza' *taurinorum* Verity, 1930—Memorie Soc. ent. ital. 9:15—Syntypes 3 males, 2 females [N. Italy]: Torino: Mte. Musime, Colli di Torino: VI, 2 VII 1923, 12 VII 1914: Gianotti [leg.].—Reiss & Tremewan (1967): *Zygaena cynarae taurinorum* (ssp.).

tenuelimbata (if)—*Zygaena filipendulae* 'form' *tenuelimbata* Verity, 1921—Entomologist's Rec. J. Var. 33:147—Type-locality not known.—Reiss & Tremewan (1967): *Zygaena filipendulae siciliensis tenuelimbata* (ab.).

tenueunco (if)—*Zygaena fulvia* 'forma' *tenueunco* Verity, 1930—Memorie Soc. ent. ital. 9:20—Type-locality not known.—Reiss & Tremewan (1967): *Zygaena loti tuscomodica tenueunco* (ab.).

tenuiorelimbata (if)—*Zygaena filipendulae* 'form' *tenuiorelimabata* Verity, 1921-Entomologist's Rec. J. Var. 33:147—Type-locality not

known.—Reiss & Tremewan (1967): *Zygaena filipendulae siciliensis tenuiorelimbata* (ab.).

tenuissimelimbata (if)—*Zygaena filipendulae* 'form' *tenuissimelimbata* Verity, 1921—Entomologist's Rec. J. Var. 33:147—Type-locality not known.—Reiss & Tremewan (1967): *Zygaena filipendulae tenuissimelimbata* (ab.).

totadiaphana (if)—*Zygaena transalpina hippocrepidis alpina totadiaphana* Turati & Verity, 1912—Boll. Soc. ent. ital. 43:218—N. Italy: Alpi Marittime: Valdieri.—Not listed by Reiss & Tremewan (1967).

TRANSFERENS (ssp, ra)—*Zygaena lonicerae* 'subspecies' *transferens* 'race' *transferens* Verity, 1925—Entomologist's Rec. J. Var. 37:117, pl. 8, figs. 48, 49—Syntypes 18 males, 7 females [Great Britain]: Hertfordshire: Tring: 17 & 23 VII 1921: Grosvenor [leg.].—Reiss & Tremewan (1967): *Zygaena lonicerae transferens* (ssp.).

*****translucens** (ra)—*Jordanita tenuicornis* 'razza' *translucens* Verity, 1946—Redia 31(1945/46):136—Syntypes 2 males [Italy]: Abruzzi: M. Sirente: Monterotondo: 1400 m: VII 1941; Gran Sasso: 1300-1500 m: 1939; Romei [leg.]: 1 male Sicilia: Madonie: M. Quacella: 21 V 1912: Fiori leg.

*****transpadana** (ra)—*Anthrocera (Polymorpha) ephialtes* 'razza' *transpadana* Verity, 1946—Redia 31(1945/46):79—Syntypes 9 males, 10 females [N. Italy: Torino]: Soria, Turbigo: 15-16 VI 1929, 15-16 VI 1930, 7 IX 1930: Rocci [leg.].—Reiss & Tremewan (1967): *Zygaena ephialtes transpadana* (ssp.).

tricingulata (if)—*Zygaena oxytropis tricingulata* 'nom. nov.' Verity, 1916—Boll. Soc. ent. ital. 47:77—C. Italy: Macerata; name for the specimen no. 874 deposited in coll. Oberthür.—Reiss & Tremewan (1967): *Zygaena oxytropis tricingulata* (ab.).

*****trinacria** (ra)—*Zygaena lonicerae* 'race' *trinacria* Verity, 1917—Bull. Soc. ent. Fr. 1917:224—Syntypes 2 males [S. Italy]: Sicilia: Lupo: Ragusa [leg.].—Reiss & Tremewan (1967): *Zygaena trifolii trinacria* (ssp.).

*****tusca** (ra)—*Zygaena cynarae* 'razza' *tusca* Verity, 1930—Memorie Soc. ent. ital. 9:15—Syntypes 14 males, 2 females [C. Italy: Toscana]: Colline di Firenze: 1-17 VII 1920-1921: Querci [leg.].—Reiss & Tremewan (1967): *Zygaena cynarae tusca* (ssp.).

*****tuscomodica** (ra)—*Zygaena fulvia* 'razza' *tuscomodica* Verity, 1930—Memorie Soc. ent. ital. 9:19—Syntypes 69 males, 20 females Italia centrale: Toscana: Colline di Firenze: 400 m: VII-VIII 1914; 11 males, 2 females same data but: Firenze: Firenzuola: 500 m: 14 VI 1916; 4 males, 3 females same data but: Palasarcio: 9 VII 1917: Verity [leg.].—Reiss & Tremewan (1967): *Zygaena loti tuscomodica* (ssp.).

uncoflabello (if)—*Zygaena fulvia* 'forma' *uncoflabello* Verity, 1930—
Memorie Soc. ent. ital. 9:20—Type-locality not known.—Reiss &
Tremewan (1967): *Zygaena loti tuscomodica uncoflabello* (ab.).

***urbis** (ra)—*Procris cognata urbis* Verity, 1946—Redia 31(1945/46):
134—Syntypes 2 males, 3 females [Italy]: Roma: Pietralata: 10 VI 1940; 2
males Roma: Fiuggi: 700 m: 15-30 VI 1936; 1 female Roma: Ponte Mam-
miolo 1 VII 1941; 1 female Roma: Portonaccio: 30 VI 1941; 1 female Roma:
Ponte Nomentano: 1 VII 1941; Verity [leg.].

***venusta** (ra)—*Procris subsolana* 'razza' *venusta* Verity, 1946—Redia
31(1945/46):129—Syntypes 1 male, 1 female [S. Italy]: Calabria: S. Fili:
800 m: primi di giugno (= early June).

viridis (if)—*Adscita alpina* 'forma' *viridis* Verity, 1946—Redia 31(1945/
46):148—Syntype 1 male [N. Italy: Alpi Marittime]: Valdieri: 27 VII
1907.

***vivax** (ra)—*Zygaena lonicerae* 'razza' *vivax* Verity, 1920—Boll. Lab.
Zool. gen. agr. R. Scuola Agric. Portici 14:38—Syntypes 13 males, 3
females Suditalia: Caserta: Massiccio delle Mainarde: Valle del Mol-
larino: 26-30 VI 1919: Querci [leg.].—Reiss & Tremewan (1967): *Zygaena
lonicerae vivax* (ssp.).

Postscript. The 3rd edition of the International Code of Zoological
Nomenclature was published in February 1985. The rules contained in
the new code do not contradict the treatment of Verity's races as proposed
by Kudrna (1983), Balletto and Kudrna (1984) and in the present
paper.

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        ital. 47:45-78.

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Egg Mass Design Relative to Surface-Parasitizing Parasitoids, with Notes on *Asterocampa clyton* (Lepidoptera: Nymphalidae)

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Abstract. The shape of an egg mass for protection of the greatest percentage of eggs from surface mortality factors, in this case parasitism, is considered using geometrical models. Egg mass design is described in terms of both numbers and stacking pattern of eggs. Egg mass design in *Asterocampa clyton* (Boisduval and Le Conte) (Lepidoptera: Nymphalidae) is compared with design attributes predicted by the models.

Introduction

Many insects deposit their eggs in masses (Hinton, 1981) including some species of butterflies (see Stamp, 1980, for overview). There are advantages to depositing eggs in masses which increase the relative fitness of those females which do so by increasing the survivorship of both the eggs and the larvae over females that do not. Among several possible advantages to clustering eggs from the standpoint of egg survivorship, there is reduction of the egg surface area (percentage of eggs) exposed to mortality factors such as parasitism and dessication. This paper considers egg mass design in response to egg mass parasitoids that attack exposed eggs.

Exposed eggs in a cluster (generally those on the surface) may be concealed in several ways: 1) with scales or accessory gland material (Anderson, 1976; Darling and Johnson, 1982), or 2) by variations in egg mass shape, which controls the percentage of eggs exposed. The degree of parasitization is also affected by the size of egg masses and their rate of discovery and utilization by parasitoids. Smaller egg masses of the gypsy moth, *Lymantria dispar* (L.), are more heavily parasitized than larger egg masses, owing to both the stacking design (shape) and number of eggs (Brown and Cameron, 1979, 1982; Crossman, 1925; Dowden, 1961; Hoy, 1976; Weseloh, 1972). A similar relationship holds for egg masses of the noctuid *Spodoptera litura* (Fab.). This moth deposits its eggs in multi-layered, scale-covered masses (Braune, 1982). Layering of eggs in masses is common among lepidopteran species whose egg masses are attacked by parasitoids. Given the physical constraints on stacking design and egg

shape, the question of optimal design for a given egg mass number can be phrased as: how many layers of what numbers and arrays of eggs hide the greatest percentage of eggs?

Models

MODEL 1: The problem of minimizing the percentage of exposed eggs is equivalent to minimizing the surface area of a geometric solid relative to its volume. Using a truncated cone as a geometrical model, one can calculate the optimal height relative to the basal radius by minimizing exposed surface area (sides and top) relative to volume. The number of layers an egg mass should have for a given clutch size can be predicted from this model (Fig. 1). The optimal shape for this model when translated into eggs is such that there should be as many layers of eggs as there are eggs in an average radius of the basal layer.

MODEL 2: Theoretical egg masses can also be generated by stacking successively smaller egg layer arrays on a basal layer (stacking of each egg onto the triad of eggs beneath it, with no overhanging eggs). Such a mass would take on the shape of a pyramid with as many sides as there were line segments formed by eggs in the circumference of the basal layer. The ideal shape for the basal layer would be a circle since this shape minimizes the circumference relative to the inscribed area. The best hexagonal approximation to a circle is a hexagon (for those with 2-7 eggs on a side) or a rounded hexagon (with a few eggs centered on each face; 8 eggs on a side and larger). Optimally built egg masses would appear as six-sided, miniature, truncated pyramids, flat-topped with steep (60 degree) sides, with the number of layers of eggs dependent on the clutch size. The number of layers giving the smallest percentage of exposed eggs (highest % hidden) should roughly be equal to the number of eggs on their respective basal sides, since the sides contain the same numbers of eggs as their respective radii (from the first model).

Table 1 shows the percentage of eggs hidden in a mass for a given base layer array, for 6 such layers in masses composed of fewer than 1000 eggs. Owing to the stacking design (it is not space-filling), these pyramidal masses overestimate the number of optimal layers relative to the model using a truncated cone, for a given base size (compare "best percentages" numbers of layers with regard to number of eggs on a basal side).

Discussion

Table 1 shows that for egg masses totalling less than 1000 eggs and up through 6 layers, more than half the eggs can be hidden in those masses which have from 5 to 11 eggs on a basal (hexagonal) side, and this can be achieved if the eggs are stacked in more than 2 layers for masses starting with 7 on a side. The best design for smaller masses is to have about the same number of layers as there are eggs on a side. Egg masses which only

have one layer hide no eggs, even though the more central eggs are somewhat less exposed.

Consider the question: if one could restack eggs after a given number were deposited, when, by adding another egg to a mass, does it become more profitable to add another layer (considering the whole range of fixed egg mass sizes)? The minimum number of eggs necessary to hide one egg in a mass is 10, so that it becomes more profitable at 9 eggs to add a tenth so that the mass forms 2 layers than add the tenth egg in a single layer.

Table 1. The number of eggs, number and percent hidden eggs (maxima), for masses based on hexagonally-shaped bottom layers, by number of layers.

$i =$ number of eggs on a side of hexagonally-shaped basal layer
$l =$ number of layers
$n =$ number of eggs in mass
$h =$ number of eggs hidden
$\% =$ percentage of eggs hidden
$* =$ best percentage for a given base

i	l	n	h	%
2	2	10	1	10.0*
3	2	31	7	22.6
	3	37	10	27.0*
	4	41	11	26.8
4	2	64	19	29.7
	3	82	31	37.8
	4	92	37	40.2
	5	101	41	40.6*
	6	105	42	40.0
5	2	109	37	33.9
	3	145	64	44.1
	4	170	82	48.2
	5	185	92	49.7
	6	201	101	50.2*
6	2	166	61	36.7
	3	226	109	48.2
	4	272	145	53.3
	5	305	170	55.7
	6	326	185	56.8
7	2	235	91	38.7
	3	325	166	51.1

	4	398	226	56.8
	5	455	272	59.8
	6	497	305	61.4
8	2	316	127	40.2
	3	442	235	53.2
	4	548	325	59.3
	5	635	398	62.7
	6	704	455	64.6
9	2	409	169	41.3
	3	577	316	54.8
	4	722	442	61.2
	5	845	548	64.9
	6	947	635	67.1
10	2	514	217	42.2
	3	730	409	56.0
	4	920	577	62.7
11	2	631	271	42.9
	3	901	514	57.1
12	2	760	331	43.6
13	2	901	397	44.1
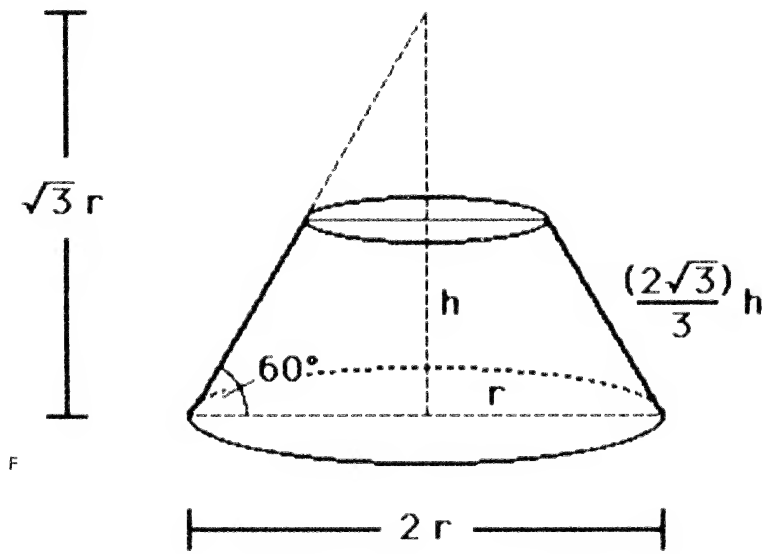
Fig. 1. Geometrical model of an egg mass by a 60 degree truncated cone (the same lateral angle produced by tetrahedral packing), with basal radius (r) and height (h).

By plotting the percentage of eggs hidden against egg mass size, for each set of masses consisting of from 2 to 6 layers from Table 1, one can roughly see the trade-off values at which successive pairs of curves cross (Fig. 2). These crossover values are the minima at which additional layers become more profitable when adding a single egg. They are, approximately: 19 (by adding one egg, rearrange from 2 layers into 3 layers at approximately 19 eggs), 67 (3 to 4), 160 (4 to 5), and 265 (5 to 6). An egg mass of 100 eggs should have 4 layers.

Most insects that deposit batches of eggs in excess of 100 per clutch do not deposit them in multi-layer masses. Among these batch-layers, few deposit their eggs in situations where the eggs are more or less exposed to the air and parasitoids. Females of the lasiocampid *Malacosoma americanum* (Fab.) produce a covering (besides eggs) for their exposed eggs (Darling and Johnson, 1982). The modelling presented in this paper probably only applies to a handful of species that for one reason or another are constrained to deposit their egg masses in very exposed situations and which do not guard their eggs or protect them using some other means. One species satisfying these criteria is the nymphalid *Asterocampa clyton* (Boisduval & Le Conte).

Notes on *Asterocampa clyton* **Egg Masses**

A. clyton deposits its eggs in large, naked, pyramidal clusters (Riley, 1874; Edwards, 1876). Roughly 2 out of every 3 egg masses of this butterfly
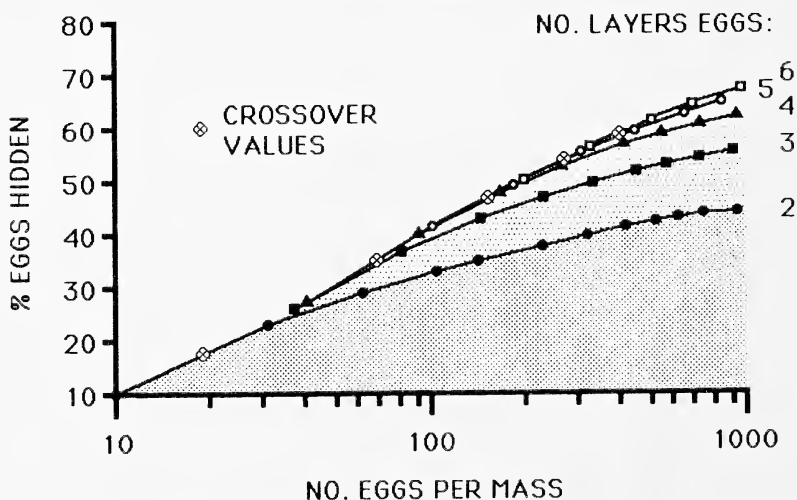
Fig. 2. Plots of the percent eggs hidden, by egg mass size, for up to 6 layers of eggs (generated from Table 1), showing the crossover values of mass size at which there is an advantage to an additional layer of eggs.

are to some degree parasitized by scelionid wasps (Friedlander, pers. obs.). From about 50 to 200 of the exposed eggs in the masses are routinely parasitized yielding levels of parasitism of over 90% in small masses to about 40% in very large masses. More than one female scelionid probably account for some of the high parasitism observed in large masses.

Table 2 shows data for egg masses of *Asterocampa clyton* compared with values predicted by modelling. Only 8 masses in the author's collection were suitable (no parasitism, or parasites/larvae not emerged) for constructing the table. Egg masses of this and a related species (*A. idyja argus* (Bates)) are known to have up to 7 layers (Friedlander, pers. obs.). The egg mass design of *Asterocampa clyton* compares favorably with predictions from the egg-stacking models.

Table 2.   Egg mass size and shape of *Asterocampa clyton* as compared with predicted design.

Size (n)	No. hidden	No. layers (obs./exp.)	% hidden (obs./exp.)
61	15	2/3	25/51
74	23	2/3	31/52
93	32	4/4	34/40
115	31	4/4	27/43
139	54	4/4	39/45
193	86	4/5	45/60
214	85	5/5	40/50
217	100	4/5	46/51

Conclusions

The composite model presented here should be applicable in all cases where clusters of a sessile life stage are subject to mortality factors affecting only the exposed (and not the hidden) units. Among the Lepidoptera the model would apply in cases where eggs were deposited in exposed masses and these eggs were subject to differential mortality based on their relative positions in the mass (exposed, hidden).

The data from the few egg masses of *A. clyton* compare favorably ($y = 79.37 - 0.11x$, $r^2 = 0.76$, $n = 8$) with those obtained by Braune (1982) for *Spodoptera litura* ($y = 76.23 - 0.07x$, $r^2 = 0.71$, $n = 39$), comparing percentage of exposed eggs with the number per mass. Statistical tests (alpha (2-tailed) = 0.05) of differences in both slope ($t = -0.81$, d.f. = 43, $p > .43$) and elevation ($t = -0.78$, d.f. = 44, $p > .44$, $p > .45$) of these regression lines resulted in no statistically significant differences being found. Braune (1982) noted that 54% of the egg batches he studied were parasitized. Small clutches were 40-100% parasitized while large clutches

experienced much lower levels of less than 50% parasitism (y = 97.04 - 0.11x, r^2 = 0.55, n= 35). The noctuid moth might be responding in the same way to parasitism as the butterfly, notwithstanding the covering of scales for its eggs.

The packing design, shape and size of the basal layer of eggs, the number, shapes and sizes of additional layers, all have an effect on the percentage of eggs exposed to mortality factors, and are therefore potentially subject to modification by natural selection. Change in the shape of egg masses is but one possible response, perhaps an unusual one among the Lepidoptera.

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Notes on the Biology of *Stalachtis susanna* (Lycaenidae: Riodininae) with a Discussion of Riodinine Larval Strategies

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Abstract. This paper describes the larval biology of *Stalachtis susanna* (Riodininae) and compares riodinine larval strategies. The differences between solitary myrmecophilous and gregarious non myrmecophilous riodinine larvae are examined. The conclusions are as follows:

1. When food resources fail, late-instar *Stalachtis* larvae enter the prepupal stage, pupate, and emerge as dwarf adults, whereas myrmecophilous larvae will resort to cannibalism.

2. Species with gregarious larvae tend to be cluster egg layers, whereas myrmecophilous species lay eggs singly, with the possible exception of the genus *Audre*.

3. Solitary larvae are more likely to have obligate myrmecophilous relationships than gregarious larvae.

4. Myrmecophilous larvae are cryptically colored whereas gregarious species are aposemetic.

5. Observations on rates of parasitism do not indicate any clearcut advantages for solitary myrmecophilous versus gregarious behaviour.

Introduction

Stalachtis susanna (Fabricius, 1787) is a medium sized riodinine butterfly inhabiting tropical and subtropical forest habitats throughout southeastern Brazil. It is particularly common in secondary or disturbed forest. *S. susanna* has a reputation for being distasteful to predators as suggested by its slow flight and bright orange colors.

Notes on the life history of *S. susanna* have appeared in D'Araujo e Silva et al. (1967) and Zikan (1953). The former records the larvae as feeding on the leaves of angelim (*Andira* sp., Leguminosae) in Minas Gerais. Zikan gives a rather brief description of the larvae, pupae and habits. He does not name the foodplant.

The purpose of this paper is to describe the larval instars and habits of *S. susanna* and to compare the larval development and survival strategies with those of other riodinine species. Observations on the biol-

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ogy of this butterfly were made in a patch of secondary forest near Barra de São Joao, Rio de Janeiro State. The climax forest in this area is typical of the transition between the low, scrubby restinga and the tropical Atlantic forest. The trees reach 10-12 meters in height and the understory consists mainly of bromelids typical of the restinga. In addition to field observations, larvae in various instars were reared and observed in the laboratory.

Description of Immature Stages

First Instar: Not available

Second Instar: Length 5.5 mm, head capsule 0.6 mm. Body rounded dorsally, flat ventrally. Color light yellow and brown with black markings. Head light brown, face with numerous small setae. First thoracic segment with a light brown saddle-shaped dorsal shield with ten long setae extending cephalad and smaller setae laterally; a spiracle on each side near junction with second thoracic segment; second and third thoracic segments with four transverse dorsal spots, each with one long and several short setae. Abdominal segments each with a black transverse bar dorsally with two long setae protruding from small tubercles and numerous short setae. Spiracles on A1-8 lateral, but more ventrally positioned on A1. On segments A9-A10 is a small dorsal plate. Duration 3 days.

Third Instar: Length 9 mm, head capsule 1 mm. Form and coloring same as second instar. Duration 4 days.

Fourth Instar: Length 13 mm, head capsule 2.5 mm. Head and first thoracic segment light orange, as are abdominal segments A9-A10, remaining segments darker orange; forelegs black. Transverse dorsal bars broken into two spots with one long white seta each; otherwise as in second instar. Duration 3 days.

Fifth Instar: Length 17 mm, head capsule 3 mm. Color overall darker orange; otherwise as in fourth instar. Duration 4 days.

Prepupal: (Fig. 1) Color turns uniform light orange with the two rows of dorsal spots reduced in size. Duration 3 days.

Pupa: (Figs. 2, 3) Length 17 mm, width at widest point (thorax) 6.5 mm. Color dark yellow with black maculation. Head yellow with two black spots and two lines between them. First segment of thorax with a dot at base of head and four short lines; thorax dorsad with a pair of black spots on each segment and two additional dots laterally; wing cases with costa and veins outlined in black. Abdominal segments each with two black spots dorsally; segments A2 and A4-A8 with an additional black spot on each side. Surface covered with small setae, each protruding from a small tubercle. Pupa secured by a silk pad and girdle. Duration 11 days.

Discussion

The foodplant of *S. susanna* in Barra de São Jõao is *Simaba glabra* Engl (Simaroubaceae), an endemic restinga plant. *S. glabra* grows as a small tree, reaching 3-4 meters in height. The glossy ovate leaves grow alternately on the branches. The *S. susanna* larvae were observed feeding on
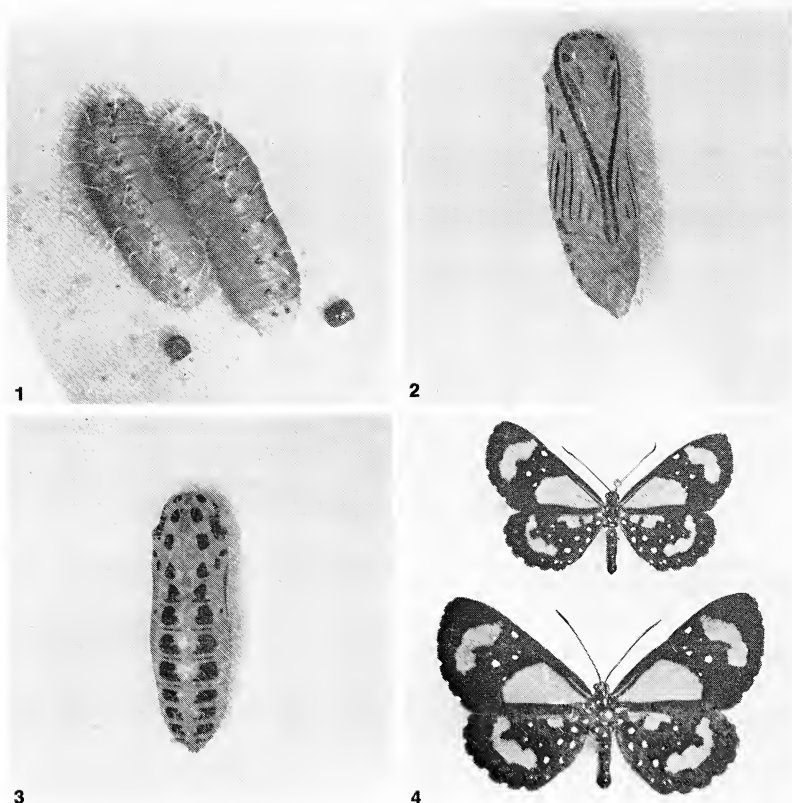
Fig. 1. Prepupal larvae.
Fig. 2. Pupa, ventral view.
Fig. 3. Pupa, dorsal view.
Fig. 3. Female imagos. Bottom, normal female. Top, dwarf female.

new growth of the plant, the older leaves were tough and leathery and avoided by larvae.

The larvae are gregarious throughout their development. They feed by aligning side by side on the edge of the leaf, then moving backwards as they eat ravenously across the leaf. The most active feeding occurs at night, early morning and evening. During the heat of the day, the larvae retire down the stem of the foodplant. Larvae of the same instar feed together, but separated from larvae of different instars. They are usually segregated on separate leaves or on different parts of the same leaf. There was no aggressive behavior observed between larvae of different instars.

The larvae grow rapidly, reaching the prepupal stage in an estimated 15 to 18 days. Prepupal larvae cease feeding, leave the young leaves of the foodplant and align side by side on the ventral surface of a leaf or stem where they remain motionless, pupating three days later.

Larval survival strategy in the face of foodplant shortages was discovered quite by accident. Three laboratory reared *S. susanna* larvae had reached the fourth instar when the available foodplant ran out. After two days of wandering around the holding jar, they retired under a dried up leaf, ceased all activity for seven days until they pupated. The pupae were smaller than those of well-fed larvae and measured 13 mm in length instead of the normal 17-18 mm. The resulting imagos, (all females), were also smaller (Fig. 4), with wing lengths of 19 mm versus 26 mm for average females. Except for size, they showed no other differences from normal females. The developmental time from fourth instar to pupation (9 days), was about the same amount of time take by feeding larvae with available foodplant. These observations suggest that if the larvae are unable to find sufficient foodplant, they will advance immediately to the prepupal stage and complete their development on nutrients stored in their tissues. This phenomenon could account for the wide variation in size encountered among adults in some *susanna* populations, which led d'Almeida to give the name *pygmaea* d'Almeida, 1922, to the smaller individuals.

This strategy contrasts sharply with that of other riodinine larvae, especially solitary myrmecophilous species. Both *Juditha molpe* (Callaghan, 1982) and *Synargus brennus* (Callaghan, in press) practice cannibalism, eating smaller larvae or pupae, when foodplant is wanting. In this way, the larger larvae could have a better chance of successfully pupating.

It became evident during the course of this study that there were other significant contrasts between gregarious riodinine larvae and myrmecophilous solitary species. These are reviewed below.

1. Oviposition. Among Neotropical riodinines, myrmecophilous species lay eggs singly on the foodplant, whereas gregarious species oviposit in clusters. In addition to *J. molpe, S. brennus* and *Menander felsina* (Callaghan, 1977), I have observed oviposition by *Nymphidium* n.sp. and *Nymphidium ascolia*, both in Colombia; and *Juditha lamis* in Brazil. Similar observations have been made by W. Benson on *Nymphidium galactina* at Jaru, Rondonia (pers. comm.). In all cases, eggs of these myrmecophilous species were placed singly, apparently at random on the foodplant, usually on the stem near petioles. Eggs were often placed on plants with larvae in various instars, suggesting that larvae, eggs and pupae are free from predation by their late instar siblings except when plant resource becomes scarce. The only apparent exception is the genus

Audre of which I have found the larvae to be solitary and myr-
mecophilous, but which is said to lay eggs in small clusters (Bruch, 1926;
Robbins & Aiello, in press).

Cluster ovipositing is associated with gregarious behavior. Examples
are *Hades noctula* (Chew and Robbins, 1984), various species of the genus
Euselasia (Otero, pers. comm.; Hoffman, 1931; Kendall, 1976).

Neotropical riodinine ovipositing behavior in this respect contrasts
strongly with that of old world lycaenids. Kitching (1981) reported that in
Australia, egg clustering in lycaenid butterflies is almost always
associated with obligate myrmecophily, whereas only a third of those
species which oviposit singly had similar relationships.

2. Gregarious vs. solitary behavior. Obligate myrmecophilous behavior
is more likely to occur among solitary larvae than among gregarious
species. All myrmecophilous larvae I have observed are solitary. In addi-
tion to *J. molpe, J. lamis, S. brennus* and *M. felsina* cited earlier, *Audre
campestris* ssp. (Southern Brazil) and *Calospila* sp. (Choco, Colombia)
are also solitary and myrmecophilous. At times, myrmecophilous larvae
will appear to be gregarious in cases where food plant resources are con-
centrated, such as the new growth on stems of foodplants, or when being
"herded" by ants, as has been observed in *Lemonias caliginea* (Ross,
1966). However, even under these circumstances, larvae will disperse as
much as possible, one or two to a leaf, and never side by side as do
gregarious larvae. Conversely, gregarious larvae apparently are not myr-
mecophilous. Examples are *Euselasia eucerus* (Brun et al., 1977,
Euselasia hygenius, notes in the Museu Nacional collection), *E.
thucydides, Hades noctula* and *S. susanna*.

3. Protection strategies. Observations on Myrmecophilous larvae sug-
gest that they are cryptically colored with a flat profile enabling them to
avoid vertebrate predation by blending with background substrate. Ants
which accompany them may also serve to discourage predators.
Conversely, gregarious species tend to be aposematic with conspicuous
profiles, achieved through their active, gregarious feeding. They obtain
protection from many predators through distastefulness (Fisher, 1930;
Chew and Robbins, 1984).

4. Parasitism. Regarding solitary myrmecophilous vs. gregarious
riodine species, there is no conclusive evidence as to which suffer more
from parasitism. I have observed parasitism by ichneumonoid wasps in
individuals of *Synargus brennus* and *Calospila* sp., in spite of the pres-
ence of ants. Although some evidence suggests that gregarious larvae suf-
fer a lower rate of parasitism (Chew and Robbins, 1984), this may not be
true for riodines. Brun et al. (1977) reported rates of parasitism up to
31.6% among gregarious larvae of *Euselasia eucerus* by an ichneumonoid
wasp (Trichogramma sp.).

Finally, the foregoing discussion does not pretend to exhaust the possible larval strategies among riodinine butterflies. It does, however, underline the lack of information concerning the biology of these butterflies and the hope that others working with life histories and biology of Neotropical diurnal Lepidoptera will give riodinine butterflies more attention.

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Oviposition by the Mistletoe-feeding Pierid Butterfly *Mathania leucothea* (Mol.) in Chile

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Abstract. Oviposition by the Pierid butterfly *Mathania leucothea* was studied in the matorral zone of central Chile. Eggs were laid on *Tristerix tetrandus* (Loranthaceae), a common parasite of two Rosaceous shrubs. Several aspects of behavior contrast with earlier studies on crucifer- and legume-feeding Pierids. Eggs were deposited in batches, on young growing tissue. The eggs turn red soon after being laid. A high percentage (30.6%) of apparently suitable hosts bore at least one egg batch. Females appear to find *T. tetrandus* by searching visually for the Rosaceous hosts, and then inspecting these (possibly by olfaction) for the mistletoe.

Introduction

Pierid butterflies have been subjected to increasing scrutiny over the past 20 years, and have become an important group in the study of insect-hostplant relationships. Nearly all this attention has been directed at a few genera: the Pierini and Euchloini feeding on Cruciferae and other Capparales, and legume-feeding *Colias*. Few studies have reported on other species, particularly in dealing with the many large tropical genera which frequently associate with hosts of quite different growth form. Nothing is known, for instance, of the ecology of the very large mistletoe-feeding genus *Delias*. I report here observations on the butterfly *Mathania leucothea* Mol., which feeds on mistletoes (Loranthaceae) parasitic on trees. The results are of considerable interest for their comparison with studies on crucifer and legume-feeding pierids. The taxonomic position of *Mathania* is unclear, but is certainly close to *Hesperocharis*, which may be related to *Euchloini*.

M. leucothea is an endemic species of central Chile, living in forested and xerophytic-shrub (matorral) areas. In the summer-arid hills east of Santiago, the adults fly vigorously among the shrubs and trees, searching for mates, nectar or oviposition sites. The flight period is long (November to late February) in the austral summer. The butterfly is relatively common at mid-elevations on the west slope of the Andes in the province of Santiago. It was studied during early February 1984, females being watched as they searched for the larval hostplant, quintral, *Tristerix* (=

Phrygilanthus) *tetrandus* R. et Pav. (Loranthaceae). All observations were carried out between curvas 1 and 14 on the road below Farellones (1400 m); few individuals are seen above this area, although stragglers do occasionally reach Farellones itself at 2500 m. *T. tetrandus* infests two of the dominants of the scrubby woods: *Kageneckia oblonga* R. et Pav. ("Bollen" or "Hueyo") and *K. angustifolia* D. Don ("Olioitto") (Rosaceae). Foliage types are illustrated in Figure 1. The parasite is easily seen when in flower, when the bright red buds can be seen through the host foliage. *T. tetrandus* tends to grow in the center of the host, sprouting from the trunk or main branches; hence, it is not easily seen when just sprouting. Nine females were watched for a total of 3124 s as they searched various trees.

T. tetrandus plants were carefully examined for *M. leucothea* eggs and larvae. Interest centered on how the female butterflies find their host, how they deposit their eggs, and how intensive a grazing pressure they may exert on the host.
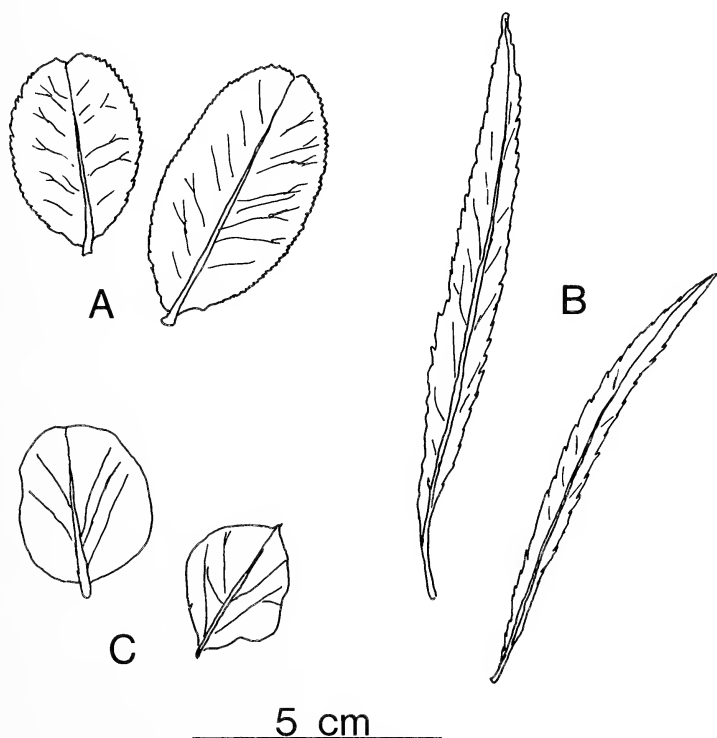
Fig. 1.   Foliage shape in **a)** *Kageneckia oblonga*, **b)** *K. angustifolia*, **c)** *Tristerix tetrandus* (sketch from herbarium specimens).

Results and Observations

Female *M. leucothea* respond initially to the sight of either of the host trees of *T. tetrandus*, the female orienting from several meters away. Each tree is surveyed for parasitic growth, usually from outside the tree. If *T. tetrandus* is present, the female may enter deep among the tree's branches, and may spend a considerable time searching for an appropriate ovipopsition site (Table 1). The behavior suggests that olfaction plays a role in detection of the larval host since females almost never enter a tree unless *T. tetrandus* is present. Females persist in examining trees with *T. tetrandus*, even if they do not initially find the larval host. Females rarely land on the tree's foliage, but do so readily on *T. tetrandus*. Such contacts are transitory—only 9 of 143 (6.3%) led to oviposition. The female, after briefly touching the host, usually continues to fly around, presumably searching for a preferred oviposition site. Egg-laying is brief when it occurs: the wings fully closed (always open during "testing" contacts), the abdomen bent under, and one to several eggs rapidly deposited.

Eggs were only seen to be laid on *T. tristerix* growing on *K. oblonga*, although they were also found on the parasite on *K. angustifolia* when those were searched (Table 2). Females usually laid more than one egg per oviposition site (Fig. 2). Some species of Pieridae usually lay many eggs at one site (e.g., *Pieris brassicae, Ascia* and *Aporia* spp.), but few species lay
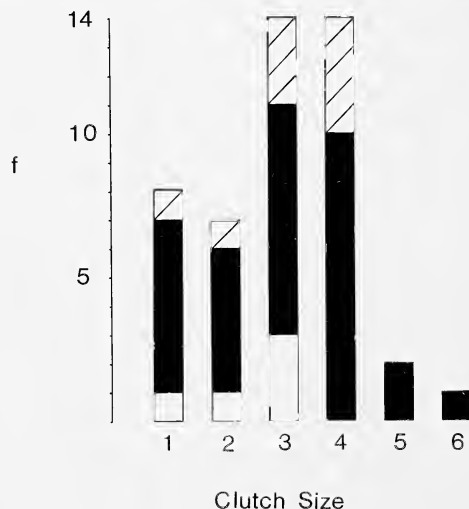
Clutch Size

Fig. 2. The frequency of different clutch sizes in *M. leucothea*. Eggs found on *K. angustifolia* (open figure), *K. oblonga* (closed) and those laid by ovipositing females (hatched) are given. The latter were observed only on *K. oblonga*. Hatched eggs are excluded.

Table 1. The number of *Tristerix tetrandus* plants encountered by females, the mean time spent searching them (s), and the number of batches and of eggs deposited on hosts growing in the two species of *Kageneckia*. Significantly more time is spent surveying trees of either species when there is parasitic growth.
(*K. angustifolia* t = 7.32, P < 0.001)
(*K. oblonga*   t = 4.98, P < 0.001)
More time is also spent scrutinizing *K. oblonga* foliage than on *K. angustofolia*.
(with *T. tetrandus* t = 5.90 P < 0.001)
(without *T. tetrandus* t = 0.68 N.S.)

| | *Kageneckia* sp. | |
	K. angustifolia	K. oblonga
No. of trees encountered		
with *T. tetrandus*	4	15
without *T. tetrandus*	17	36
Mean time spent searching trees (s)		
with *T. tetrandus*	46.0	102.7
without *T. tetrandus*	9.5	12.3
No. of batches laid	0	9
No. of eggs laid	0	28

batches of the sizes described here. *Pieris napi* L. (England) and *Colias vauthieri* (Chile) individuals may lay several eggs together if their respective hosts are rare (unpublished data), but *T. tetrandus* did not appear host limited during this study.

M. leucothea eggs are white when first laid, but turn red within a day or so, as in many other Pieridae. Shapiro (1981) linked red egg coloration to detection and deterrence of oviposition by other females. No evidence for or against Shapiro's hypothesis could be detected in this study. Note, however, that *T. tetrandus* plants appear large enough to support many larvae (though preferred tissues may be in short supply—see below); hence, there should be no competition among larvae or selection for deterrence of other females. Also, the presence of red eggs in a species taxonomically distant to those studied by Wiklund and Ahrberg (1978) and Shapiro (1981), suggests that the trait may be ancestral and may not reflect local adaptation at all; a similar view is put forward by Hayes (1985). This appears to be the first record of easily detected red eggs in a batch-laying species.

Oviposition was concentrated upon a very limited area of the host (Table 3) and white eggs were found only upon the youngest areas of

growth. This finding suggests females chose apical growth, which may be better suited to larval growth. Among Pieridae, similar behavior has been noted in *Pieris rapae* L. (Jones et. al., 1982) and *Anthocharis cardamines* L. (Wiklund and Ahrberg, 1978). The preference for young growth leads to a clustering of batches upon *T. tetrandus* plants without flowers (Table 4); the resultant frequency distribution of batches on plants without flowers indicates strong clumping of batches (variance: mean ration = 8.85/1.21 = 7.31:1). Clumped egg distributions occur in a large number of pierid species (reviwed by Courtney and Courtney, 1982); such distributions can result from butterflies tending to discover the same hosts—these are the first data suggesting that choice of oviposition sites also causes clumping.

Miscellaneous Observations

1. On two occasions females were seen to "interact" with each other in the manner of courting males. In both cases one of the females, which had discovered a host-plant, appeared to chase the other (A. M. Shapiro observed similar behavior in *Danaus plexippus* [L]). Since 22 of 72 (30.6%) of apparently suitable *T. tetrandus* shoots bore eggs, it is suggested that optimal host oviposition substrate may be limited. Red eggs, quasi-territoriality and batch oviposition by females might thus all be linked to low availability of host material.

Table 2.   The numbers of *T. tetrandus* plants, and of *M. leucothea* batches and eggs found in a sample of *Kageneckia* trees. Trees were sampled by walking from curva 3 up the road to Farellones, examining every tree adjacent to the road; sampling ceased when 100 *K. oblonga* plants had been examined. *K. angustifolia* plants are less often infested by *T. tetrandus* and the parasites growing in that host are less often attacked by *M. leucothea* (hatched eggs are not included here).

| | *Kageneckia* sp. | |
	K. angustifolia	*K. oblonga*
No. of trees discovered		
with *T. tetrandus*	6	31
without *T. tetrandus*	29	69
No. of *T. tetrandus*	7	39
No. of *T. tetrandus* with eggs	3	21
Mean No. of *M. leucothea* eggs per *T. tetrandus* plant	1.7	2.5
per plant with eggs	4.0	4.6

Table 3. The distribution of *M. leucothea* eggs of different color stages and ages, upon different tissues of *T. tetrandus*.

	Number of eggs			Number of batches
	white	red	hatched	
Open flowers	—	—	—	—
Closed flowers	——	1	—	1
Stems and leaves > 10 cm from apex	—	55	64	41
Stems and leaves < 10 cm from apex	—	17	18	12
Apical stems and leaves	23	7	—	13

Table 4. The effect of *T. tetrandus* age status upon *M. leucothea* oviposition.

Status of *T. tetrandus*	No. of Plants	No. of Plants with Eggs	No. of Batches
> 20% of flowers open	10	0	0
< 20% of flowers open	7	2	2
No flowers open	29	22	35

2. Less time was spent by females searching *K. angustifolia* than *K. oblonga* (Table 1). This may reflect the similarity between the foliage of *T. tetrandus* and *K. oblonga*, although *K. angustifolia* trees are also often small, requiring less search time. One female was of particular interest: having oviposited on *T. tetrandus* in a *K. oblonga* tree, she then immediately discovered two *K. angustifolia* and one *K. oblonga* growing tangled together. Only 13 s were spent searching *K. angustifolia* foliage but 98 s in *K. oblonga* (*T. tetrandus* was not present on any of the trees) and the female persistently returned to the latter foliage. This may indicate a short-term learning effect, as shown in other butterflies (Stanton, 1983; Papaj and Rausher, 1983).

3. *T. tetrandus* plants were very heavily attacked by several herbivores, including a batch-laying moth. Many ants and lacewing larvae (potential predators) were also seen. Survival of *M. leucothea* appeared very poor: only 11 of 32 (13.4%) of hatched eggs still had a larva nearby. Despite apparent poor early instar of survival by *M. leucothea*, the effect of butterfly grazing on the plant may be disproportionate to the amount of tissue consumed, since grazing is concentrated on young tissues.

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Book Review

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Nekrutenko, Y.P., 1985. Hardback ca. A4 size, 152 pages, 24 col. pls., 123 figs.,
Naukova Dumka, Kiev (U.S.S.R.). Rbl. 2.30

The Crimean Peninsula forms a part of the northern Black Sea coast. Politically, it belongs to Ukraine, one of the republics of the U.S.S.R., situated in southeastern Europe. The European Ukraine and Russia are poorly known parts of Europe from the lepidopterological point of view. Every new publication concerning moths and butterflies is therefore most welcome. The present book, which deals with the butterflies (Papilionoidea) and skippers (Hesperioidea) exceeds all expectations. It contains a treatment of all 112 species inhabiting the Crimean Peninsula (classified to subspecies). Every distinct species (subspecies) is illustrated in color (probably the best color plates of butterflies ever produced in the Soviet Union!). Male and female(!) genitalia are shown by means of line drawings, and accompanied by carefully selected line drawings depicting the wing venation of some taxa. The descriptive part includes the following features for every species: external characters and genitalia of male and female; essential bibliographical references and synonyms; distribution; biology, and, where necessary, a paragraph concerning their conservation. Additional features of the book are an extensive general part and keys facilitating the identification to subspecies. The book is, in comparison to what usually comes from the U.S.S.R., uncommonly well printed. Some more critical readers might suggest that the amount of information not directly related solely to the Crimea is not in the right proportion to the Crimea-specific data. Such judgment is, of course, a matter of opinion. It must be borne in mind that the "general" information is surely most useful for all students of Russian Lepidoptera, who, apart from Korshunov's check-list and Kurentsov's book on the butterflies of the Far East, have no up-to-date handbook dealing with such aspects. Nevertheless, it is a pity that the specific information on the distribution of butterflies in the Crimea is concise rather than comprehensive, that is, underrepresented. The inclusion of distribution maps, a descriptive check-list of localities and photographs of some characteristic biotopes would have added to the importance of this book. Color illustrations show specimens enlarged (but not all to the same scale) instead of the usually preferred life size. The author's list of Papilionoidea and Papilionidae is attributed to "[Leach], 1815"—I wonder why not Latreille, 1809? The extensive bibliography is most useful. The author certainly deserves our congratulations.

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INSTRUCTIONS TO AUTHORS

Manuscript Format: Two copies *must* be submitted (xeroxed or carbon papered), double-spaced, typed, on 8½ x 11 inch paper with wide margins. Number all pages consecutively and put author's name at top right corner of each page. If your typewriter does not have italic type, underline all words where italics are intended. Footnotes, although discouraged, must be typed on a separate sheet. Do not hyphenate words at the right margin. All **measurements** must be metric, with the exception of altitudes and distances which should include metric equivalents in parenthesis. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as example: 4. IV. 1979 (day-arabic numberal; month-Roman numeral; year-arabic numeral). Numerals must be used before measurements (5mm) or otherwise up to number ten e.g. (nine butterflies, 12 moths).

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References: All citations in the text must be alphabetically listed under Literature Cited in the format given in recent issues. Abbreviations must conform to the *World List of Scientific Periodicals.* Do not underline periodicals. If four or less references are cited, please cite in body of text not in Literature Cited.

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Legends should be separately typed on pages entitled "Explanation of Figures". Number legends consecutively with separate paragraph for each page of illustrations. Do not attach to illustrations. Retain original illustrations until paper finally accepted.

Review: All papers will be read by the editor(s) & submitted for formal review to two referees. Authors are welcome to suggest reviewers, and if received, submit name & comments of reviewers.

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THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

A New Squash Borer from Mexico (Lepidoptera: Sesiidae)

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Abstract. A new species of *Melittia* (Lepidoptera: Sesiidae) is described from southern Mexico. Females superficially resemble *M. snowii* Hy. Edwards in size and coloration, but males resemble small males of *M. grandis* (Strecker). This species is a borer of wild mesophytic squash vines at altitudes exceeding 1500 m. Scale patterns and colors, genitalia, egg morphology and hostplant usage are compared among the North American species of the genus.

Introduction

Eichlin (1975) provided brief descriptions of the species of *Melittia* Huebner (Sesiidae) in North America north of Mexico, with notes on their biologies (with maps, keys, and color figures). These moths feed on wild and cultivated squash and gourds (Cucurbitaceae, mainly *Cucurbita* spp.). Additional collecting in southern Mexico yielded another moth in the genus worthy of description, belonging with those already depicted by Eichlin.

After careful examination of all described New World *Melittia* (Friedlander, unpublished honors thesis, Oberlin College; Duckworth and Eichlin, 1973a, 1978), it was concluded that the taxon herein described represents a distinct species. It is a pleasure to name this new species after Thomas D. Eichlin, who provided training and assistance in my early studies in sesiid taxonomy.

The specimens were collected in mid-July of 1983 and 1984 in southwestern Mexico by members of the Department of Entomology, Texas A&M University, in 2 separate expeditions led by Dr. J. C. Schaffner. Initial collection turned up one newly emerged and mated female in Colima (9 mi. ne. Comala). Subsequent collecting in this part of Mexico yielded additional specimens of both sexes in association with the hostplant. The types (male holotype, female allotype; Jalisco, 5 km w. Atenquique, 11 July 1984) will be deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., and paratypes distributed equally among that collection, the insect collection at Texas A&M University and that of the UNAM in Mexico City.

Fig. 1. Adult male, holotype, dorsal view.
Fig. 2. Adult female, allotype, dorsal view.

Melittia eichlini new species Friedlander

Adult Male (Fig. 1): Wingspan 20-26 mm, including fringe on FWs; length of FW along costal margin 9-12 mm. Body length approximately 10-13 mm, from anterior bases of antennae to fringe of scales on last visible abdominal segment (8). Males appear as small male *M. grandis* (Strecker), but with virtually no orange scaling on either the abdomen or legs.

Head: Frons smooth-scaled, dark gray, with white scaling laterally to compound eyes, very dark gray shelf of scales attached under antennal bases, shelf projecting laterally of eyes; vertex with dark gray scales overlain with dark gray hair-scales emerging from occiput dorsally; occiput scales laterally behind eyes, white; **lateral ocelli** prominent, clear with finely granular surface, appearing whitish; **compound eyes** slightly concave (in outline) next to antennal bases, with golden sheen on dark gray background; **pilifers** coppery, covering base of naked, brownish orange haustellum; **haustellum** with about 6 pairs of evenly spaced setae laterally at base between labial palps; **labial palps** smooth-scaled above, rough below, white at base, becoming light yellow apically; dark gray to black hair-scales mixed apically and ventrally on last 2 segments; some dark gray scales mesally, forming a streak to tip; **antennae** each with approximately 50 segments, pectinate with clumps of long black ciliae on first 35 or so flagellar segments, scaled with dark gray above, unscaled below and on most of unciliated, reddish brown segments; tips of antennae small with dozen, projecting black setae; white scaling in patches at anterolateral bases of pectinations on middle 20 flagellar segments, yellow scaling posterolaterally in streak towards tip; basal segment (pedicel) scaled with white laterally and ventrally.

Thorax: Prothoracic collar smooth-scaled, dark gray with very dark gray, yellowish white-tipped scales dorsally, overlain with light yellow hair-scales; **mesothorax** similar dorsally, but with large dark gray scales overlying bases of FWs and metathorax, long gray and pale yellow hair-scales posterolaterally; **metathorax** similar dorsally, but with long whitish hair-scales laterally; thorax dark gray laterally beneath wings except (yellowish) white thoracic collar; **forelegs**: coxae dark gray and yellow anterodorsally, with white and dark gray scales at apex (over trochanters), femora yellow dorsally mixed with dark gray ventrally; tibiae and tarsi dark gray and yellow, banded (yellow basally, dark gray apically); epiphysis long, bare, reddish brown; terminal tibial spines black; **mesothoracic legs**: femora dark gray anteriorly, yellow dorsally with long (pale) yellow hair-scales ventrally; trochanters covered by smooth dark gray scales with a

few pale yellow scales mixed, long white hair-scales posteriorly; tibiae bushy-scaled with light yellow and dark gray mixed, brownish orange spines projecting through; terminal spurs long, dark gray basally, white apically, anterior one half length of posterior one; terminal spines long, black; tarsi dark gray scaled except yellowish white at bases of each segment giving banded appearance; short, dark reddish brown spines in rows ventrally; **metathoracic legs**: femora whitish with dark gray scaling mixed anterodorsally, with long whitish hair-scales ventrally; trochanters covered by smooth dark gray scales with a few white scales mixed, long white hair-scales posteriorly; tibiae and basitarsi rough-scaled with white dorsally, white bushy-scaled (dorso-)posteriorly, interrupted by similar black scales at level of mid-spurs; similarly black-scaled (ventro-) posteriorly, white scales (ventro-) anteriorly; puff of white scaling anteriorly at apex of tibiae; both pairs of spurs black-scaled with whitish near tip (tips bare), but rough-scaled with white (lateral spurs) or black (mesal spurs) ventrally; rest of tibiae banded white and dark gray as in mesothoracic legs; **forewing (FW)** dark gray-scaled overlain with very dark gray, yellowish white-tipped scales, fringe composed of long spatulate dark gray scales in 3 ranks (lengths); ventrally, dark gray apically with considerable light orange scaling basally, especially along veins; anal margin rolled down; **hindwing (HW)** scaled with dark gray on veins only and at ends of cells and bases of anal cells; fringe same as on FW; vein A1 broadly scaled; costal margin rolled up, with whitish scales dorsally; ventrally same but with orange scaling mixed anteriorly and pale yellow at anterior base.

Abdomen: Each segment dark gray-scaled overlain with very dark gray, yellowish white-tipped scales dorsally (in broad longitudinal stripe), posterior fringe of broad dark gray scales which reflect light at certain angles, emerging under row of brownish orange flat spines on visible segments 2-8 (these spines fit into sockets; see Naumann, 1977); pale yellow and gray hair-scales scattered dorsally, especially on segments 4-8; dark gray scaling (dorso-)laterally on segments 2-8, bordered with white on each segment posteriorly; dark gray and white mixed ventrally, invaded with whitish, especially laterally; posterior fringe scales pale gray on each segment; white at base laterally on segment 1; anal fringe dark gray dorsally, white ventrally (both mixed with the other somewhat).

Genitalia (Figs. 11-14): **Saccus** of moderate length, 1.3 mm; **valves** long, 1.9 mm, somewhat falcate with saccular fold, apices filled with black setae inwardly, long-scaled outwardly, each with inward basal pit; **uncus** bifid, with narrow "V"-shaped indentation, **socii** black-haired, the whole effect appearing like a flared cloven hoof; **aedeagus** long, 2.4 mm.

ADULT FEMALE (Fig. 2): Wingspan 22-24 mm, including fringe on FWs; length of FW along costal margin 9-12 mm. Body length approximately 11-14 mm, from anterior bases of antennae to fringe of scales on last visible abdominal segment (7). Superficially similar to *M. snowii* Hy. Edwards in size and coloration above, but with yellow below; with rough, light-tipped, dark gray scaling over FWs and body as in *M. grandis* (Strecker). Similar to male, but with following differences.

Head: Labial palps white at base, becoming brilliant orange-yellow apically; **antennae** scaled with dark gray above, mixed dark gray and yellow below; yellow scaling increases towards tip becoming a lateral pre-apical streak; some white scaling occurs mesodorsally about two-thirds towards tip for about 7 segments.

Thorax: Mesothorax dorsally with few pale yellow spatulate scales above bases of HWs and mixed laterally on metathorax; **metathorax** with long pale yellow

hair-scales laterally; thorax dark gray laterally beneath wings except (yellowish) white thoracic collar and a few yellow scales laterally in front of FWs; **forelegs**: coxae yellow anterodorsally, with white and dark gray scales at apex (over trochanters), femora yellow dorsally mixed with dark gray ventrally; tibiae and tarsi dark gray mixed with yellow dorsally with yellow ventrally, yellow decreasing apically to give a banded appearance (yellow basally, dark gray apically); terminal tibial spines black; coxae, femora mixed dark gray and pale yellow posteriorly; femora with posteroventral, long yellow hair-scales; tibiae yellow posteriorly; tarsi whitish ventrally; **mesothoracic legs**: femora yellow anterodorsally with long (pale) yellow hair-scales ventrally; trochanters covered by smooth dark gray scales with few pale yellow scales mixed, long white hair-scales posteriorly; tibiae bushy-scaled with yellow, brownish orange spines projecting through; terminal spurs long, dark gray basally, yellowish white apically with bare tips, anterior one half length of posterior one; terminal spines long, dark reddish brown with lighter tips; tarsi dark gray-scaled except yellowish white at bases of each segment giving banded appearance; **metathoracic legs**: femora yellow with dark gray scaling mixed anterodorsally, with long (pale) yellow hair-scales ventrally; trochanters covered by smooth dark gray scales with a few pale yellow scales mixed, long white hair-scales posteriorly; tibiae and basitarsi rough-scaled with yellow dorsally, vivid orange bushy-scaled (dorso-)posteriorly, interrupted by similar (bluish) black scales at level of mid-spurs; similarly black-scaled (ventro-)posteriorly, yellow scales bordered with orange (ventro-)anteriorly; puff of white scaling anteriorly at apex of tibiae; both pairs of spurs black-scaled with whitish near tip (tips bare), but rough-scaled with white (lateral spurs) or black (mesal spurs) ventrally; rest of tibiae banded yellowish white and dark gray as in mesothoracic legs, with brush of orange basally to white dorso-apically; **forewing (FW)** ventrally dark gray apically with more yellow antero- and orange posterobasally.

Abdomen: Vivid orange scaling (dorso-)laterally (in broad longitudinal stripes) on segments 2-7; dark gray ventrally, invaded with lightened mixture of orange, especially laterally; anal fringe dark gray dorsally, orange ventrally (both mixed with the other somewhat).

Genitalia (Fig. 15): **sternite 7** weakly sclerotized, composed of 2 longitudinal bands, each 2.2 mm long; **sclerite 8** divided dorsally, projecting anteromesally in 2 points length dorsally 0.8 mm; anterior apophyses 1.4-1.5 mm long, more than a dozen setae around posterior edge of sclerite; **post-ostiolar sclerite** relatively narrow, "U"-shaped with trailing ends dorsally like bicycle handlebars, concave in the direction of **ostium; ductus bursae** 2.7 mm long, membranous with small (0.3 mm long) sclerotized ring just posterior to ductus seminalis (1.3 mm beyond ostium); **bursa copulatrix** elongate (2.8 mm long by 0.9 mm at widest), the last one fourth slightly less wide, forming an indistinct lobe, such as seen on inflated, elongate balloons, bursa finely granular (no signum); sperm case inside elongate (1.9 mm) with stalk into ductus; **anal papillae** not heavily sclerotized, 0.6 mm long, hairy (long hairs 0.3 mm long), posterior apophyses 1.7-1.8 mm long; whole "ovipositor" extends 3.3 mm beyond posterior edge of tergite 7.

Egg (Figs. 4, 7, 8): Eggs typical of *Melittia* species (Chittenden, 1908; Eichlin, 1975; Williams, 1913), flat, lying on their sides, anterior pole with micropylar region facing laterally along long axis; oval in shape as viewed from above, having a rim around base (side by which they are fixed to a substrate such as a leaf blade); at most 1.00 mm long by 0.72 mm wide by 0.44 mm high at micropylar end; micropylar region round, flat (raised in some specimens at center into small button);

sculpture obscure, finely granular with a hint of hexagonal reticulation. As viewed with scanning electron microscopy (SEM), eggs measure roughly 0.8 mm long by 0.6 mm wide, punctated (aeropyles?), except along ventral rim and micropyle, with slightly raised polygonal network of ridges (most easily seen along external sides of rim and forming micropylar rosette); rim not flared, but undercut ventrally; micropylar rosette small, in 2-3 ranks with 5-8 petals centrally.

Range (Fig. 16): Southwestern Mexico from Jalisco to Michoacan at altitudes above 1500 m. Specimen data as follows: Colima: 9 mi. ne. Comala, July 17-18, 1983, Kovarik, Harrison, Schaffner [T. Harrison, collector], one female; Jalisco: 0.5 and 8 mi. w. junc. 54 & road to Parque Nacional Volcan de Colima, near Atenquique, 11-12 July 1984, Schaffner, Woolley, Carroll, Friedlander [T. Friedlander, J. Schaffner, collectors], 6 males, 2 females; Jalisco: 8 mi. s. Autlan, 8 July 1984, Schaffner *et al.* [J. Schaffner, T. Friedlander, collectors], 4 females. Suspected of belonging to this species, based on notes (Friedlander, unpub.), but not included in the type series: Michoacan: Morelia, 15 July 1956, R. & K. Dreisbach, 2 males, one female [Michigan State Univ. collection]; Michoacan: Carapan, 1 July 1963, W. A. Foster, one male [Univ. Calif., Berkeley collection]; Jalisco: 5 mi. w. Atenquique, 25 July 1963, J. P. Donahue, one female labelled "in copula" [Michigan State Univ. collection].

Hostplant: *Cucurbita sororia* Bailey (tentative determination by D. Decker and H. Wilson, Dept. Biology, TAMU), a mesophytic member of the squash genus. The hostplant was found in disturbed to cultivated situations in montane areas north of Colima, Mexico, at about 2000 meters. At the collection site south of Autlan, seedling plants were found growing on a recently cleared roadside hill, not at all obviously planted. Female moths were found flying in the immediate vicinity and eggs were found on the plants, both on the leaf blades and on the stem near the bases of the vines. Oviposition was observed. At the site northeast of Comala no moths were found in 1984, but the hostplant was abundant on both sides of the road for about a kilometer, and plants were seen growing in adjacent cultivated fields, in pure stands, as if they had been cultivated. Plants along the road to the Parque Nacional Volcan de Colima near Atenquique lined the road for a shorter distance and occurred in areas of habitation higher up the mountain. Male moths were observed on blades of squash leaves and also, rapidly flying over the plants. One mated pair was observed on a leaf blade, and another female was found resting on a leaf.

Discussion

This species is sexually dimorphic in coloration. Males are similar in size to those of *M. snowii*, but are similar to males of *M. grandis* in color, except that the orange of the latter is replaced by white. Females are similar in size and coloration to those of *M. snowii*.

A superficial color comparison of the female of *M. eichlini* with *M. snowii* (specimens from central Texas) revealed the following differences. *M. snowii* is everywhere lighter gray (and on the whole, grayer) with less contrast to the white-tipped scales. *M. eichlini* has contrasting white-tipped scales such as are found in *M. grandis*. The antennae of *M. snowii* are uniformly dark gray; the compound eyes are without a golden sheen;

the labial palps are white below. *M. eichlini* has light-colored scaling ventrally on the antennae, and has the white spots dorsomesally as do female *M. calabaza* Duckworth and Eichlin; it has eyes with a golden sheen and orange-yellow palps ventro-apically. *M. snowii* foreleg coxae are white dorsally and dark gray elsewhere; the femora are yellow-orange dorsally and dark gray elsewhere; the tarsi are not banded; orange replaces the yellow found on *M. eichlini* mesothoracic legs; there is no orange on the metatarsi. *M. eichlini* females have, on the whole, much more colorful legs. The dorsal gray abdominal stripe is narrower in *M. snowii*.

M. grandis is everywhere more orange, and is normally much larger than *M. eichlini*. The Arizona variety (female) of *M. grandis (hermosa* Engelhardt) has a continuous gray stripe down the center of the abdomen dorsally, but is alternating gray and orange at the sides.

Some female specimens of *M. snowii* retain orange scaling in the cells of the HW, much like the western race of *M. gloriosa* Hy. Edwards, but this trait is not expressed in *M. grandis*, or in the female specimens of *M. eichlini*.

Engelhardt's (1946) description of *M. snowii* states that the collar is "lustrous blue-black," which differs from the Texas specimens, as well as the new species, which have dark gray collars. The collar of *M. grandis* is mostly orange.

The genitalia of *M. eichlini* are the smallest of all, equaled only by those of *M. snowii*. Male genitalia (Figs. 11-14) are quite similar in form to those of *M. grandis*. There is a ridge on the *edge* of the valve opposite the sacculus which distinguishes *M. grandis* from *M. eichlini*. There are also slight differences in the shape of the uncus, which might better be attributed to differences in preparation of the genitalia for viewing, but which might hold true in long series. Genitalia of *M. snowii* have blunt valves with little saccular ridge development, and the uncus is broadly indented in the shape of a "U". Other members of the genus differ considerably in the shape of the uncus and/or valves (see: e.g., Duckworth and Eichlin, 1973b: Fig. 3).

In the female genitalia (Fig. 15) of *M. eichlini* the shape of the postostiolar sternite is like that found in *M. grandis* and *M. gloriosa*, different from the broad chevron found in both *M. snowii* and *M. calabaza* (Duckworth and Eichlin, 1973b: Fig. 6). *M. snowii* lacks the sclerotized ring of the ductus, found in the other species (only weakly indicated in *M. grandis*). The shape of the bursa in *M. eichlini* is more like that of *M. grandis* than other species, being up to 3 times as long as wide, whereas *M. snowii* has one only 2 times as long. *M. calabaza* and *M. gloriosa* have a bursa two and a half times as long as wide.

This species shares the character "split sternite 7" with *M. grandis*, a condition quite different than that found in *M. snowii* (whole, with weak indentation posteriorly), or in *M. calabaza* (whole, but weakly sclerotized in a longitudinal strip along median). *M. gloriosa* has a short, rounded

sternite 7.

The eggs of *M. eichlini* differ from other species mainly in size, being, on the average, slightly larger than those of *M. snowii*, but smaller than those of the other species. Hexagonal reticulations are more pronounced in *M. calabaza* and *M. cucurbitae* than in *M. eichlini*, but at the macroscopic level the eggs agree well in design with other *Melittia* (except *M. gloriosa*, which lacks the bottom rim).

As seen in the SEM micrographs, *M. snowii* eggs (Figs. 3, 9) are similar in size, perhaps slightly more elongate, than those of *M. eichlini*. The micropylar rosette is larger than in *M. eichlini*, clearly in 3 ranks, with 6 or 7 petals centrally. *M. grandis* eggs (Fig. 5) are similar in form but are more than one and a half times larger. *M. gloriosa* eggs are also larger, but these lack a rim. *M. calabaza* eggs (Figs. 6, 10) are more broadly oval and one and a third times longer, with flared rims. The polygonal reticulations are stronger than in the other species. The micropylar rosette is larger than in *M. eichlini*, in 3 ranks, with 6-9 petals centrally.

The known hostplant relationships of North American species of *Melittia* are shown in Table 1. There are at least 5 other species of *Melittia* in Mexico for which there is no documented host data.

M. snowii is a stem- and petiole-gall maker on a tap-rooted perennial gourd, the xerophytic *Cucurbita foetidissima* H.B.K. *M. grandis* and *M. gloriosa* are root-borers on the same plant, the latter having a wider host

Table 1.   Known hostplant relationships among North American squash vine borers.

Melittia spp.	*Curcurbita* spp.; etc.
calabaza	*maxima*[1], mixta[1], moschata*[1], pepo*[1], texana[1]*
cucurbitae	*[andreana][2], [ecuadorensis][2], [ficifolia][2], maxima*[2-5], mixta[2], moschata[2-4], [okeechobeensis][2], pepo*[2-5], texana[2], Echinocystis lobata[3]*
eichlini	*sororia[1]*
gloriosa	*foetidissima[6-8], palmata[6,7], Echinocystis fabacea[6-8]*
grandis	*foetidissima[6,7]*
snowii	*foetidissima[6-8]*

*preferred hosts
[1]Friedlander, unpub. data; [2]Howe and Rhodes, 1973; [3]Chittenden, 1908; [4]Howe, 1949; [5]Whitcomb and Garland, 1948; [6]Eichlin, 1975; [7]Engelhardt, 1946; [8]Williams, 1913.

range. *M. eichlini* is a stem-borer on a mesophytic species of *Cucurbita*, tentatively determined to be *C. sororia*. Members of the squash-vine borer complex (Becker and Eichlin, 1984) are stem-borers of cultivated squash, mainly in *C. maxima* and *C. pepo*.

It appears that *Melittia eichlini* is closest to *M. grandis* morphologically, and might be derived from its ancestors. Alternatively *M. grandis* could be directly derived from *M. eichlini*-like ancestors. In either case, a host species shift has taken place and either stem-boring or root-boring, respectively, should be considered a specialization.

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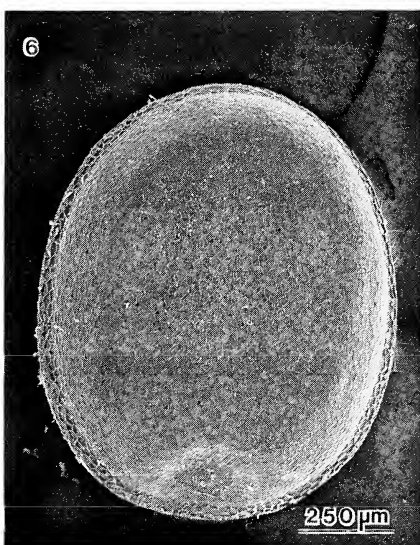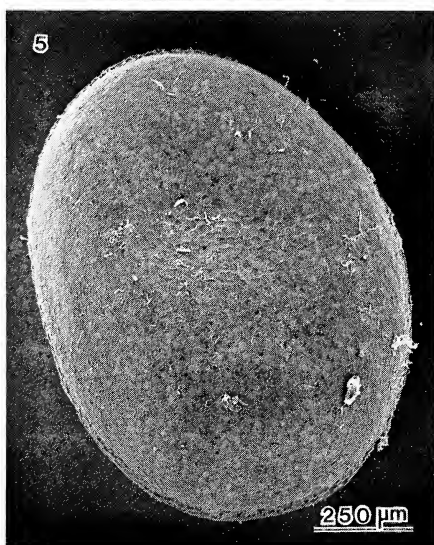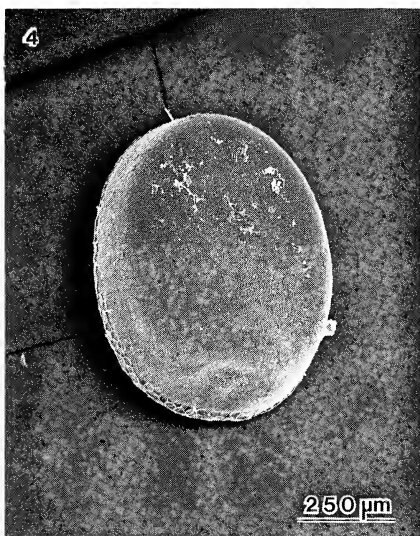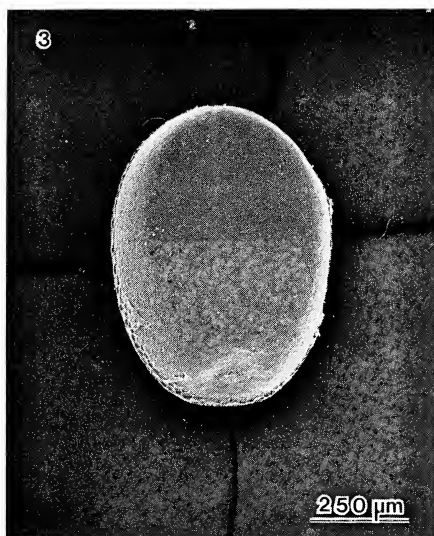
Fig. 3.   Egg of *M. snowii*, upperside, view of micropylar end; note: basal rim, narrowing of micropylar end.

Fig. 4.   Egg of *M. eichlini*, upperside, view of micropylar end; note: basal rim, broad oval outline.

Fig. 5.   Egg of *M. grandis*, upperside, view of micropylar end; note: basal rim, rounded top.

Fig. 6.   Egg of *M. calabaza*, upperside; note: broad basal rim, broad oval outline, flat top.
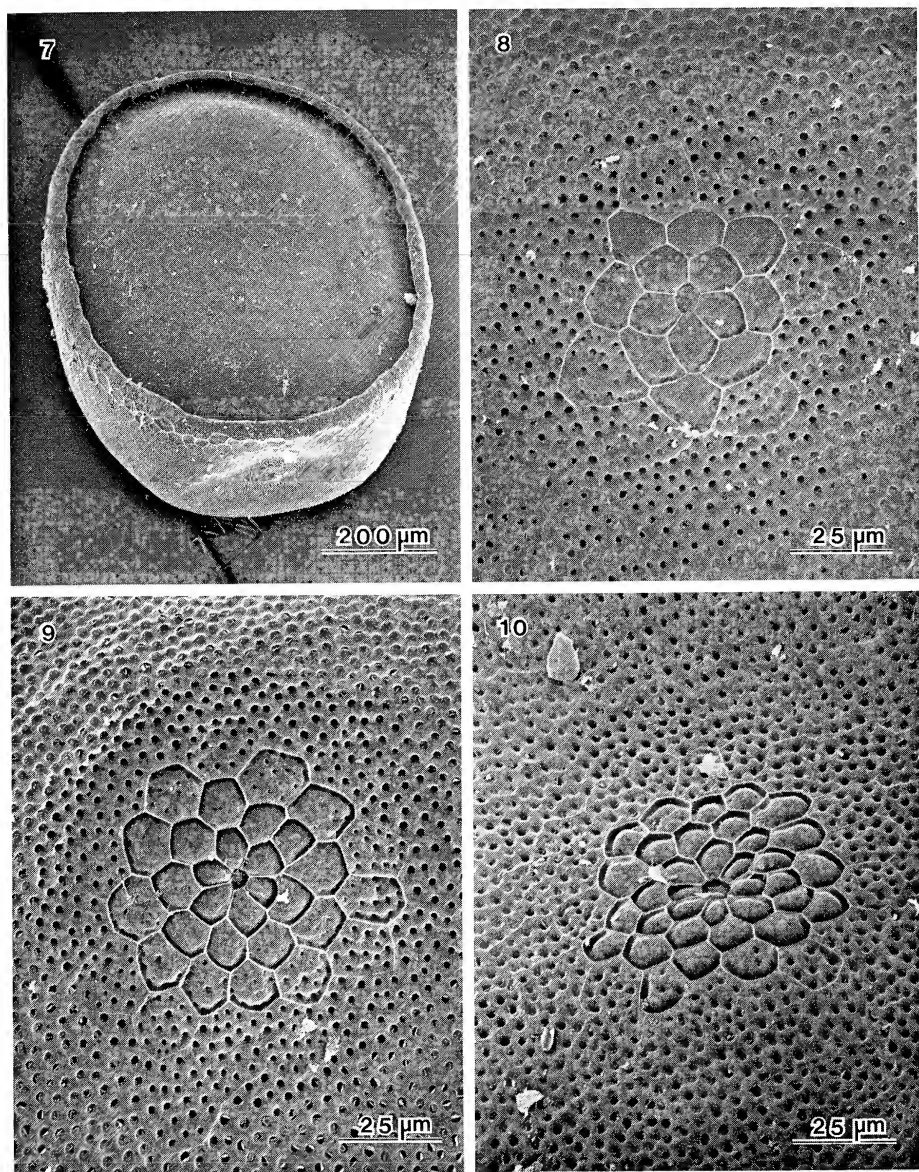
Fig. 7.   Egg of *M. eichlini*, underside, view of micropylar end; note: rolled over rim.

Fig. 8.   Egg of *M. eichlini*, micropyle; note 2 ranks of petals in rosette.

Fig. 9.   Egg of *M. snowii*, micropyle; note: 3 ranks of petals in rosette.

Fig. 10. Egg of *M. calabaza*, micropyle; note: 3 ranks of petals in rosette.
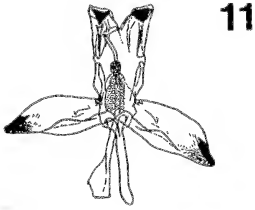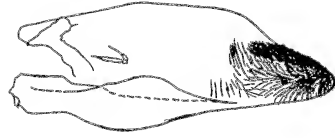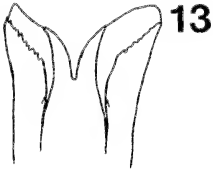
Fig. 11. Male genitalia, ventral view; valves spread.
Fig. 12. Left valve of male genitalia, inward view; note: absence of costal
          ridge (arrow).
Fig. 13. Dorsal view of uncus, male genitalia.
Fig. 14. Aedeagus of male genitalia.
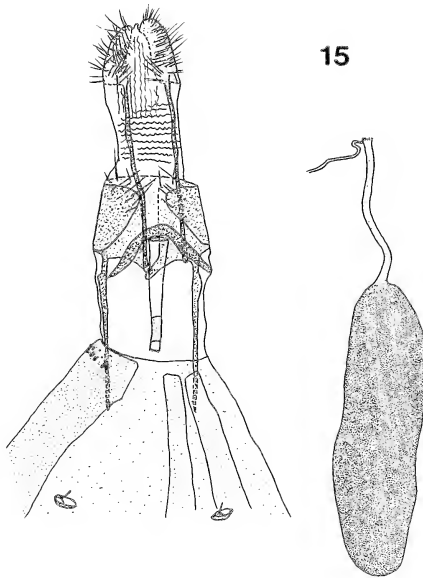
Fig. 15. Female genitalia, ventral view; ductus bursae broken at level of
          ductus seminalis.
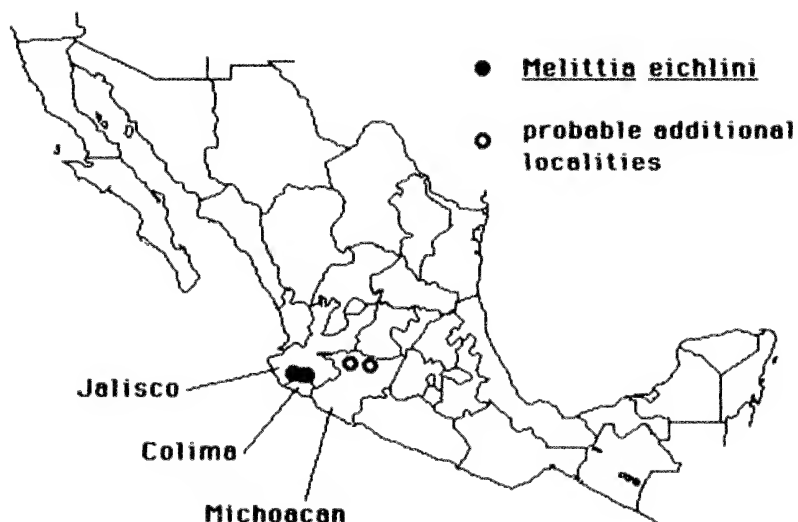
Fig. 16. Map of known distribution of *Melittia eichlini*.

A Tribute to Professor Zdravko Lorković

Zdravko Lorković is one of the finest persons I have known. I first met him in 1958 at the Cold Spring Harbor Symposium on population genetics. Ernst Mayr arranged his trip to the United States to call attention to the generally undiscovered but very forward looking and exciting work Zdravko was doing at the time with the *Erebia tyndarus* group. His classic paper on vicariant species relations was published in the Cold Spring Harbor Symposium 23 (1958). We have been promised an updated revision and expansion of this work in the next year.

Professor Lorković's other work includes extensive studies on chromosome mechanics in hybridization and hybridization studies such as reported here. The paper in original form was given at the SEL Wageningen meeting in April 1986. A complete bibliography of Professor Lorković has been published in *NOTA Lepidopterologica* (1985, 8:293-298) citing 86 papers.

Professor Lorković was born in Zagreb at the turn of the century and has lived there continously since. After completing his doctorial studies he remained at the University of Zagreb, where he was professor on the Veterinary Faculty until 1952 when he transferred to the Medical Faculty for biology until his retirement in 1970.

Professor Lorković, we dedicate this volume of *The Journal of Research on the Lepidoptera* to you for your outstanding accomplishments in basic biological/genetic research in the field. We are particularly pleased that we can offer a tribute, not a memorial. We note you have been more productive in the second half of your career than the first. Your interest has given you a long and fruitful life. We look forward to many more works.

Rudi Mattoni

Hostplant Records and Natural History Notes on Costa Rican Butterflies (Papilionidae, Pieridae & Nymphalidae)

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Abstract. Hostplant records for 209 species of butterflies in the families Papilionidae, Pieridae and Nymphalidae are reported from various habitats throughout Costa Rica to provide a basis for understanding fine-scale hostplant relationships of neotropical butterflies at the population level. Notes on egg, clutch-size, larval behavior, larval feeding, oviposition behavior, and hostplant microhabitat are given. New and unusual hostplant families and errors in the hostplant literature are discussed, and the possiblilities of unrecognized sibling species masquerading under a single species name are indicated.

Introduction

To students of butterflies it has become evident that hostplant relationships play an increasingly important role in butterfly biology. Hostplant data have been used in developing classifications and systematics at the family, subfamily, genus, and species levels (Müller, 1886; Singer et al.,1983; DeVries et al.,1985), and in some cases the hostplant has been used as a character in naming populations (e.g. Murphy & Ehrlich, 1984). Hostplant data are of paramount importance for elucidating broad-scale evolutionary patterns of host use among systematic lineages (Brues, 1924; Ehrlich & Raven, 1965; Benson et al., 1976), for understanding butterfly ecology at the community (Gilbert, 1984) and population (Ehrlich, 1984) levels, for the dynamics of host-breadth and host shifts (Singer, 1983, 1984), and for the development of mimicry theory (Gilbert, 1983) and ecological chemistry (Brower, 1984). In short, hostplant relationships are a basis upon which we rest many of our ideas about butterflies.

Taken as a whole, it appears from surveys of literature records that hostplant relationships are well understood for the majority of the systematic lineages of butterflies (Ehrlich & Raven, 1965; P. Ackery, in prep.), particularly at higher systematic levels. However, this is not true with respect to specific butterfly faunas at the genus and species levels. Perhaps the only places on earth where such relationships are well known,

but not completely known at these levels are in the U.S.A., England, parts of northern Europe and Japan. In these areas fine-scale hostplant data are available for entire faunas which can be used to develop systematic and ecological studies with a critical degree of resolution. In all other areas of the world such data are not available, and this is especially so in the tropics. Although the tropics contain the greatest diversity of butterfly species, compared to temperate regions, hostplant relationships of butterflies are poorly known, and least known of all in the neotropics. If we are to gain an understanding of the butterflies of the neotropics comparable to our knowledge of the temperate regions, it is important to have a more complete picture of hostplant relationships than currently exists. This is a tall order considering that the neotropics contain a butterfly diversity greater than any other region on earth (DeVries, 1986). One very useful method is to develop hostplant lists for butterfly faunas of specific areas.

During a long term and continuing study of the butterfly fauna of Costa Rica I have had the opportunity to rear a number of species, as well as the good fortune to work with colleagues who, although involved in studies of their own, have provided me with hostplant records to augment my work. I here summarize the hostplant records for 209 species of Costa Rican butterflies in the families Papilionidae, Pieridae and Nymphalidae reared between 1976 and 1982 by my colleagues and myself. The purpose of this paper is to provide a starting point for eventually understanding fine-scale hostplant relationships at the population level for neotropical butterflies. Natural history information is provided for both butterflies and hostplants in coded form along with each hostplant record. In the remainder of this paper I highlight some new and unusual hostplant records, point to instances where there may be several species currently placed under one name, and draw attention to what I believe to be errors in previous literature. Additional hostplant records of Costa Rican butterflies and an analysis of the ecological patterns of hostplant use which are evident in the present paper will be discussed in a future publication (DeVries, in prep.).

Materials and Methods

Except where indicated, all hostplant records presented (Appendix I) have resulted from a larva feeding on a plant and developing into an adult. All records are from field collected eggs or larvae, except where otherwise noted. Oviposition records are indicated as such, the butterflies have been positively identified with a voucher specimen taken at the time of oviposition, or in a few cases, determined on the wing with the use of binoculars. Therefore, the vast majority of records reported here have voucher specimens in the collection of the author or the person responsible for the record.

Butterfly Nomenclature. The nomenclature follows DeVries (1986) which is modified and refined from DeVries (1983). Additional systematic references useful

for Costa Rican butterflies may be found in Ackery and Vane-Wright (1985), De-Vries et al. (1985), Higgins (1981), Jenkins (1983) and Singer et al. (1983).

Plant Determinations. The hostplants in Appendix (I) are for the most part positively determined to genus (many to species), but in a few instances it was only possible to determine the plants to family due to undescribed taxa or insufficient plant material. The following people have lent their expertise in determining the hostplants: H. Bold, W. Burger, I. A. Chacon, R. Foster, L. D. Gomez, W. Haber, B. Hammil, L. Gilbert, G. Hartshorn, D. H. Janzen, S. Knapp, R. Marquis, R. Pohl, L. Poveda and F. G. Stiles. Useful references for indentification of plants of Costa Rica include: Allen (1956), Burger (1971, 1977), Croat (1978), Daniels and Stiles (1979), Janzen and Leisner (1980) and Stiles (1980).

Coded Information in Appendix I: Explanations for the coded sequences in Appendix I are found in Tables I, II and III. This information is found in a series of columns located to the right of each butterfly taxon and corresponds to: hostplant indentity, locality of record and who reared the butterfly, egg clutch-size, oviposition behavior, larval behavior, larval feeding and binomic notes concerned with the ovipositing butterfly and microhabit of the hostplant respectively. Further details on localities, habitats, and butterfly biology in Costa Rica are found in DeVries (1986).

All hostplant records reported here are from Costa Rica except those coded *AA and *KS. These come from Barro Colorado Island, Panama and augment Costa Rican records. Except for those hostplant records marked with an asterisk and a set of initials preceding the locality code, all records are those of DeVries. The initials refer to records of the following people: AA = A. Aiello, IC = I. A. Chacon, RC = R. Cubero, SK = S. Koptur, LEG = L. E. Gilbert, WH = W. Haber, DJ = D. H. Janzen, JM = J. Mallet, RM = R. Marquis, KS = K. Steiner, MCS = M. C. Singer, FGS = F. G. Stiles, and TR = T. Ray.

Comments

The hostplant records in Appendix I completely corroborate the pattern of relationship between hostplants and butterflies as described by Ehrlich and Raven (1965). There are, however, a few records in Appendix I which deserve special comment because they either represent hostplant families not reported in Ehrlich and Raven (1965), or they indicate a need for further study within the neotropical butterfly fauna as a whole. These records are briefly discussed here by butterfly family.

Papilionidae: The record of *Papilio cleotas* feeding on Moraceae requires confirmation since no papilionid species is known to feed on this plant family anywhere in the world. Hostplant records in the literature frequently report that *Papilio cresphontes* and *P. thoas* both utilize Rutaceae and Piperaceae as larval hostplants. Based on field experience and the data presented here I believe that such records are misidentifications of the butterfly species; the species are extremely similar in appearance. In Costa Rica *P. cresphontes* larvae feed only on Rutaceae,

and conversely, *P. thoas* larvae feed only on Piperaceae.

Pieridae: The records of *Catasticta* and *Pereute* feeding on Loran-thaceae and the behavior and morphology of larvae and pupae suggest a close affinity to the extensive Old World genus *Delias*. The records also further amplify those reported in Ehrlich and Raven (1965). However, I believe the reference of *Pereute* feeding on the Lauraceae (Jörgensen, 1932) is in error (DeVries, 1982). I also believe the record of *Perrhybris lypera* feeding on Lauraceae is a plant misidentification (see Young, 1980, 1982; DeVries, 1982). The records of *Aphrissa statira* feeding on Bignoniaceae are very unusual for the Pieridae, and suggest either a chemical convergence between certain Bignoniaceae and Caesalpiniaceae or that there is more than a single species under the name *A. statira*.

Nymphalidae: The records of *Agrias amydon* on Erythroxylaceae represent an unusual hostplant family for the subfamily Charaxinae. It is further notable because of commercial interest in both the butterfly and chemistry of secondary chemicals of the hostplant genus. The record of *Zaretis itys* feeding on Piperaceae is unusual since its usual hostplants are Flacourtiaceae in the same habitat. Several interesting records are reported from the Nymphalinae. In my experience, the larvae of *Eunica monima* feed only on Burseraceae. I believe that the original record of this species feeding on Rutaceae (Dyar, 1912) represents a misidentification of the hostplant which subsequently became embedded in the literature. Muyshondt (1975) stated that Müller (1886) was in error for reporting *Diaethria marchalli* to feed on*Trema* (Ulmaceae) and said that in El Salvador he only found this species feeding upon Sapindaceae. In Costa Rica, *Trema* is the only hostplant for *D. marchalli* of which I am aware, suggesting that either the butterfly switches hostplant families in areas north of Costa Rica, or that there are two species of butterfly involved here. Data reported here suggest either that certain species of *Adelpha* are highly polyphagous, or that there are cryptic species involved under the same name (e.g. *A. boreas, A. celerio, A. heraclea*). *Adelpha melanthe*, on the other hand, changes hostplant family from east to west in Costa Rica, but all are closely allied within the Urticales. In the sub-family Satyrinae the record of *Megeuptychia antonoe* feeding on Cyclanthaceae is unusual, but Cyclanthaceae has recently been demon-strated to be a host of *Caligo* in Costa Rica as well (I. A. Chacon, pers. comm.). The record of *Euptychia insolata* feeding on Neckeraceae is the first record for any butterfly to utilize a member of the Bryophyta as a lar-val hostplant, although some members of the genus are known to feed on Lycopsida (Singer et al., 1983). Lastly, the records of *Pierella* and *Cissia confusa* on Poaceae, Marantaceae, Palmae and Heliconiaceae indicate a high degree of polyphagy, mostly within the same habitat.

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Table 1. Numerical Codes for Hostplant Families in Appendix I.

1 Acanthaceae	17 Erythroxylaceae	33 Poaceae
2 Amaranthaceae	18 Euphorbiaceae	34 Poaceae:Bambusoidea
3 Annonaceae	19 Fabaceae	35 Rubiaceae
4 Aristolochiaceae	20 Flacourtiaceae	36 Rutaceae
5 Asclepidaceae	21 Heliconiaceae	37 Sapindaceae
6 Bignoniaceae	22 Hernandiaceae	38 Selaginellaceae
7 Brassicaceae	23 Lauraceae	39 Simaroubaceae
8 Bromeliaceae	24 Loranthaceae	40 Solanaceae
9 Burseraceae	25 Marantaceae	41 Tiliaceae
10 Caesalpiniaceae	26 Melastomataceae	42 Tropaeolaceae
11 Capparidaceae	27 Mimosaceae	43 Turneraceae
12 Caricaceae	28 Moraceae	44 Ulmaceae
13 Compositae	29 Neckeraceae	45 Umbelliferae (=Apiaceae)
14 Cyclanthaceae	30 Palmae (=Arecaceae)	46 Urticaceae
15 Cyperaceae	31 Passifloraceae	47 Verbenaceae
16 Ericaceae	32 Piperaceae	

Table 2. Codes for Rearing Localities Cited in Appendix I.

AT = Atenas (Al)
BLH = Bajo la Hondura (SJ)
BAR = Barranca (PUN)
BCI = Barro Colorado
    Island (PAN)
CDM = Cerro de la Muerte (SJ)
CURR = Curridibat (CAR)
COP = Copey (SJ)
CAN = Cañas (GUAN)
CAR = Parque Braulio Carrillo (SJ)
CVDO = Parque Corcovado (PUN)
EST = Estrella de Cartago (CAR)
ELROD = Finca el Rodeo (SJ)
GOL = Golfito (PUN)
HER = Heredia (HER)
LALT = Finca las Alturas (PUN)

LS = Finca la Selva (HER)
MV = Monte Verde (PUN)
PATT = Patarra (SJ)
RCN = Rincón de Osa (PUN)
SV = San Vito de Java (PUN)
SRNP = Parque Santa Rosa (GUAN)
SJ = San José (SJ)
TUR = Turrialba (CAR)
UCR = Universidad de Costa Rica (SJ)
VTUR = Volcán Turrialba (CAR)
VBVA = Volcán Barva (HER)
VSM = Volcán Santa Maria (GUAN)
VDS = Virgen del Socorro (AL)
VM = Volcán Miravalles (AL)

Costa Rican Province Codes are: (AL) = Alajuela, (CAR) = Cartago, (GUAN) = Guanacaste, (HER) = Heredia, (PUN) = Puntarenas, (SJ) = San José. The code (PAN) = the country Panamá.

Table 3.   Codes Used for Eggs, Larvae and Hostplant in Appendix I.

Eggs and Oviposition

S = eggs laid singly
C = eggs laid in clusters
    1 = female may oviposit several times on same plant.
    2 = female usually oviposits only once on a plant.
    3 = female always oviposits several times on same plant.

Larval Behavior

S = solitary
G = gregarious
    1 = larvae feed on new, then old leaves.
    2 = larvae will feed on all leaves.
    3 = larvae feed only on young leaves.
    4 = larvae feed only on older leaves.
    5 = larvae feed on plant parts other than leaves.

Hostplant Microhabitat

1 = female oviposits on plants occurring in open areas.
2 = female oviposits on plants occurring in forest.
3 = female oviposits on plants occurring at forest or riparian edges.
4 = female oviposits on plants occurring in forest light gaps.

Appendix I. Reading from left to right the information in this appendix is divided into five columns corresponding to: 1) butterfly taxa, 2) hostplant, locality and authorships of rearing, 3) clutch-size of eggs and frequency of oviposition, 4) larval behavior and feeding and 5) microhabitat of hostplant and natural history notes. Explanations for the coded sequences are found in the text and in Tables 1, 2 and 3.

Species	Hostplant & Locality	Egg & Larval Data		Bionomic Notes of Host and Butterfly

FAMILY: PAPILIONIDAE

GENUS: **Battus**

polydamas L.

	Aristolochia (4)			
	grandiflora SJ	C	G1	All hostplants are 3 and 4. Egg clusters range
	anguicida SRNP	C	G1	from 5 to 10.
	undetermined LS			

belus
varus Kol.

	Aristolochia (4)			
	grandiflora SJ, TUR.	S1	S1	Hostplants are 3, 4 and riparian edges.
	undetermined LS.	S1	S1	
	undetermined CVDO	S1	S1	
	undetermined SV	S1	S1	

crassus Cr.

	Aristolochia (4)			
	veraguensis CVDO	C	G1	Hostplants are 2, 3, 4 and riparian edges.
	undetermined LS	C	G1	Egg clusters range from 20 to 40 eggs.

GENUS: **Parides**

photinus Dbldy.

	Aristolochia (4)			Hostplants are 3 and 4 provided they receive
	pilosa ELROD, AT.	C	G2	direct sunshine. Plants are usually juvenile
				growing along the ground.

childrenae Gray

	Aristolochia (4)			
	tonduzii LS.	S1	S1	Hostplants are all 2, either young or old, pro-
	undetermined *RM LS	S1	S1	vided they have vigorous new growth.

sessostris
zestos Gray

| | *Aristolochia* (4) | | | This rearing was of six mature larvae all on the |
| | undetermined VM | ? | ? | same juvenile plant, eating all leaves. |

Species	Hostplant			Notes
iphidamus Fab.	*Aristolochia* (4)			
	veraguensis CVDO, AT.	S1	S1	Hostplants are 2, 3, 4 and riparian edges where
	af. grandiflora CAR.	S1	S1	microhabitats have been slightly disturbed.
	tonduzi LS.	S1	S1	Plants are either juvenile or mature.
	undetermined *JM CVDO	?	S1	
lycimenes Boisd.	*Aristolochia* (4)			
	maxima *IC VSM	?	S1	Hostplants are 3 and 4, either juvenile or
	undetermined *RM LS.	?	S1	mature with new shoots.
arcas	*Aristolochia* (4)			
mylottes Bates	anguicida SRNP	S1	S1	All hostplants are 2, 3, 4, either young or
	grandiflora VDS.	S1	S1	mature plants and usually close to the
	tonduzii LS	S1	S1	ground.
	undetermined CAR	S1	S1	
GENUS: Eurytides				
epidaus Dbldy.	*Annona* (3)			
	reticulata SRNP	S1	S1	Females oviposit on saplings or mature forest trees occurring in sunny places within the forest.
euryleon	*Annona* (3)			
clusoculis But.	glabra MV.	S1	S1	Both hostplant genera are 1, 2, 3, 4 and may
	Guatteria (3)			range from seedlings to mature forest trees. It is
	oliviformis VSM	S1	S3	of interest that only young leaves of *Guatteria* are acceptable to larvae.
branchus Dbldy.	*Annona* (3)			
	reticulata *DJ (81-SRNP-249)	?	?	Janzen reared this species from a solitary larva. No information on leaves or plant condition.
orabilis Butler	*Guatteria* (3)			
	tonduzii VDS	S3	?	The female lays many eggs in the axils of new growth leaves of large subcanopy trees along riparian edges. I have observed oviposition a number of times over the course of three years but have not reared larvae past third instar.

Species	Hostplant & Locality	Egg & Larval Data		Bionomic Notes of Host and Buttfly
GENUS: **Papilio**				
cresphontes Cr.	*Citrus* (36)			
	several species SV, AT, GOL, PAT.	S1	S1	All *Citrus* = 1, *Zanthoxylum* = 2, 3 on medium sized trees in the forest. Janzen's record is from a late instar larva.
	Zanthoxylum (36)			
	setulosum SRNP, CAN, CVDO	S1	S1	
	Essenbeckia (36)			
	litoralis *DJ (79-SRNP-106)	S1	S1	
thoas				
nealces R & J	*Piper* (32)			
	tuberculatum SRNP, AT			All plants are either 1 or 4 depending on the species and the habitat. All eggs are S2; all larvae are S1.
	sancti-felicis LS			
	marginatum *DJ (81-SRNP-1046)			
	amalago *DJ (81-SRNP-827)			
	auritum LS			
	multiplinervium *RM LS			
	reticulatum *JM CVDO			
	friedrichsthalii *JM CVDO			
	undetermined VDS			
polxenes				
stabilis R & J	*Apium* (45)			
	leptophyllum SJ,VDS,VB, PAT,COP, TUR.	S1	S2	Both hostplants are 1, females oviposit on young and mature plants.
	Foeniculum (45)			
	vulgare MV.	S1	S2	
cleotas				
archytas Hop.	*Sorocea* (28)			
	trophoides *WH VM	?	?	Haber reared this species from a solitary mature larva feeding on mature leaves. This represents a very unusual record for the Papilionidae.
victorinus				
vulneratus Butler	*Persea* (23)			
	americana *WH MV	?	?	Haber reared this species from a solitary late

instar larva feeding on all leaves of an open grown tree.

birchalli Hew.

Hernandia (22)

Hostplant		Codes	Notes
didymanthera LS	S2	S3	All of the hostplants are 4, but plants in light gaps are in deep shade. The females oviposit on saplings about 1 meter tall.
undetermined CAR	??	S3	
undetermined *RM LS	S?	S3	

anchisiades
ideaus Fab.

Cassimiroa (36)			
edulis SJ	C	G1	*Cassimiroa* and *Citrus* are 1 and from previous experience in Santa Rosa I assume that *Zanthoxylum* is either 1 or 4. Females oviposit on young or mature plants.
Citrus (36)			
various species CAR,CVDO,TUR,LS, PAT	C	G1	
Zanthoxylum (36)			
setulosum *DJ (79-SRNP-163)	C?	G1	

FAMILY: PIERIDAE

GENUS: **Dismorphia**

amphiona
praxinoe Dbldy.

Inga (27)

undetermined CAR	S1	S2	Hostplants are all 2, 3, or 4 in shady areas. Females oviposit on saplings or medium sized trees in the understory. Larvae usually eat old leaves but all are acceptable.
undetermined LS	S1	S2	
sapindoides *SK TUR	S1	S2	
densiflora *SK TUR	S1	S2	

eunoe
desine Hew.

Inga (27)

undetermined VB	S1	S?	I have observed oviposition but have not reared larvae. The female oviposited four eggs on the same sapling in shady understory of cloud forest habitat.

zathoe
pallidula But. & Dru.

Inga (27)

undetermined BLH	S1	S3	Hostplants are 2, 3 and 4 depending on the habitat. All plants are saplings.
undetermined CAR	S1	S3	
densiflora *SK MV	S1	S3	

Species	Hostplant & Locality	Egg & Larval Data		Bionomic Notes of Host and Butterfly
crisia				
lubina But.	*Inga* (27)			All hostplants are 2, 3 and 4 and range from
	undetermined EST	S1	S1	understory saplings to mature canopy trees.
	undetermined *SK MV	S1	S1	Females will lay from 5 to 15 eggs on the
	Pithecellobium (27)			same plant depending on the size of the plant.
	brenesii *WH MV	?	S1	
zaela	*Inga* (27)			Hostplants are 3 and 4 and all are saplings in the
oreas Sal.	undetermined CAR	S1	S2	understory or in shady light gaps.
GENUS: **Lieinix**				
nemesis G & S	*Inga* (27)			Hostplants are 3 and 4. This species can ap-
	mortonia *SK MV	S1	S3	parently feed on a variety of species of *Inga*
	longispica *SK MV	S1	S3	but is restricted entirely to new growth leaves.
	brenesii *SK MV	S1	S3	
	densiflora *SK MV	S1	S3	
GENUS: **Anteos**				
clorinde Godart	*Cassia* (10)			Hostplants are 1 and may be young or mature.
	emarginata SRNP	S1	S2	
mareula Fab.	*Cassia* (10)			Hostplants are 1 and may be young or mature.
	emarginata SRNP	S1	S1	
GENUS: **Phoebis**				
argante Fab.	*Cassia* (10)			All hostplants are 1 except *Pentaclethra* which
	biflora SRNP	S1	S1	may be 4. All range from saplings to mature
	fruticosa LS	S1	S1	trees and may be seedlings in *Pentaclethra*.
	Pentaclethra (27)			
	macroloba LS	S1	S1	

Species	Hostplant			Notes
philea L	*Inga* (27)			
	vera *DJ (79-SRNP-387)	?	S	
	ruiziana *JM CVDO	?	S	
	Cassia (10)			
	grandis SJ	S1	S1	All plants are 1 or 3 and range in size from young to mature forest trees.
	alata SJ	S1	S1	
	leptocarpa *DJ (79-SRNP-398)	?	S?	
	hayesiana *DJ (82-SRNP-4)	?	S?	
	fruticosa *RM LS	?	S?	
rurina But.	*Cassia* (10)			
	fruticosa *RM LS	S1	S3	Marquis records this species from numerous larvae feeding only on new leaves of an isolated tree in an open area.
sennae Cr.	*Cassia* (10)			
	biflora SRNP			
	obtusifolia *DJ (79-SRNP 407)	?	S?	All hostplants are 1 or 3 and usually sapling trees.
GENUS: Aphrissa				
statira Cr.	*Callichlamys* (6)			
	latifolia *DJ (81-SRNP-72)	?	S3	Janzen reared this species from solitary late instar larvae only on new leaves. These records are the first for the Pieridae feeding on the Bignoniaceae.
	"Woody vine" (6)			
	undetermined *DJ (79-SRNP-10918)	?	S3	
GENUS: Eurema				
mexicana Feld.	*Diptysa* (19)			
	robinoides HER	S1	S3	Hostplant is 1 or 3 in bright sunshine. Plants range from saplings to mature trees.
albula Cr.	*Cassia* (10)			
	fruticosa LS	S1	S1	Hostplant is 1 and ranges from saplings to mature trees. Mature larvae are able to feed on old leaves.

Species	Hostplant & Locality	Egg & Larval Data		Bionomic Notes of Host and Butterfly
dina West.	*Picramia* (39) *alleni* ELROD *quaternaria* SRNP	S1 S1	S3 S3	Hostplants are 2, 3 or 4 provided there is some shade. Plants range from saplings to mature trees.
daira Feld.	*Aeschynomene* (19) undetermined SRNP, CAN.	S1	S1	Hostplant 1, usually in recently disturbed pastures and roadsides.
GENUS: **Catasticta**				
teutila Dbldy.	*Dendropthora* (24) *costaricensis* VTUR, CDM	C	G2	The hostplant is an epiphytic parasite. There has been confusion in the literature, because the host tree rather than the parasite was often taken to be the hostplant of the butterfly. Females oviposit on mature hostplants occurring on mature emergent canopy trees or on large remnant trees in pastures.
theresa Butler	*Antidaphne* (24) *viscoides* COP	C	G2	The hostplant is an epiphytic parasite of *Alnus* (Betulaceae) that occurs along riparian edges. Egg clusters range from 10 to 50 eggs.
nimbice bryson G & S	*Struthanthus* (24) undetermined *IC PAT	?	G2	Chacon reared this species from a mass of early instar larvae feeding on all leaves. The hostplant is an epiphytic parasite of forest trees.
GENUS: **Pereute**				
cheops Staud.	*Antidaphne* (24) *viscoides* COP	C	G	This is a single cluster of eggs after I observed oviposition. Larvae have not been reared past first instar.

charops Boisd.	"mistletoe" (24) undetermined LALT	C	G	I have repeatedly watched, with binoculars, several females oviposit large clusters of eggs on what was certainly Loranthaceae. In addition I have seen large groups of larvae feeding on leaves of the same epiphytic parasite. These larvae descended the tree trunk and pupated on the tree trunk. The hostplants were growing on large emergent canopy trees along riparian edges.
GENUS: Hesperocharis				
crocea Bates	*Struthanthus* (24) undetermined *IC SJ	?	?	Chacon reared this species from a small aggregation of late instar larvae feeding on all leaves. The hostplant is an epiphytic parasite.
GENUS: Itaballia				
demophile J & T	*Capparis* (11) *indica* SRNP, BAR *frondosa* *WH CAN	S1 ?	S1 S1	Hostplants are 3 and 4 and are mature woody shrubs.
caesia tenuicornis B & D	*Podandrogyne* (11) *pulcherrima* BLH, CAR, COP, SV	S1	S1	Hostplant is 2 or 3 usually along riparian edges. Females oviposit on young and mature plants. Larvae also feed on flower buds.
GENUS: Pieriballia				
mandella noctipennis B & D	*Capparis* (11) *pseudocacao* *WH MV	?	S?	Haber reared this species from a solitary late instar larva feeding on all leaves. The plant occurred as a small understory tree.

Species	Hostplant & Locality	Egg & Larval Data		Bionomic Notes of Host and Butterfly
GENUS: Perrhybris				
pyrrha Fab.	*Capparis* (11)			
	isthmensis CVDO	C	G2	Hostplant is 2 and 4, either young or mature tree.
lypera Kollar	*Capparis* (11)			
	pittieri LS	C	G2	Hostplants are 2, 3 or 4, ranging from seedling to sapling plants. Egg clusters range from 10 to 50 per leaf.
	pittieri *WH LS	C	?	
	undetermined *LEG LS			
GENUS: Ascia				
monuste L.	*Lepidium* (7)			
	undetermined SJ	S1	S1	Hostplant is always 1 and in areas of recent disturbance. Both young and mature plants are acceptable to ovipositing females. The *Crataeva* record is an oviposition as viewed through a Questar telescope.
	Crataeva (11)	S1	?	
	undetermined *LEG CVDO			
josepha G & S	*Capparis* (11)			
	indica SRNP, CAN	S1	S1	Hostplants are 3 and 4 and may be sapling or mature trees.
	incana *DJ (81-SRNP-1086)	?	S1	
GENUS: Leptophobia				
aripa Boisd.	*Nasturtium* (7)			
	officinale SV, EST, CAR.	C	G2	Both hostplants are riparian edge species and usually grow in bright sunshine. Plants may be young or mature.
	Tropaeoleum (42)	C	G2	
	maritzianum VDS, CAR.			

FAMILY: NYMPHALIDAE
SUBFAMILY: CHARAXINAE

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GENUS: **Archaeoprepona**

demophon L.

Nectandra or *Ocotea* (23)
undetermined LS — S1 — S1 — Hostplants are 3 or 4 and range from young to mature trees. Larvae rest on frass chains.

Ocotea (23)
veraguensis *DJ (81-SRNP-218) — ? — S1

amphimachus
gulina Fruh.

Persea (23)
americana VB — S1 — S1 — Hostplants may be 1, 2, 3 or 4 depending on the habitat and range from seedlings to mature forest trees. Larvae rest on frass chains.

Phoebe (23)
undetermined *WH MV — ? — S?

GENUS: **Prepona**

laertes
octavia Fruh.

Inga (27)
ruiziana *JM CVDO — ? — S? — Records are from late instar larvae which fed on all leaves of a forest edge tree.

GENUS: **Agrias**

amydon
philatelica DeVr.

Erythroxylum (17)
havanense * DJ (80-SRNP-209) — ? — S2 — Both records are from solitary late instar larvae feeding on all leaves. The hostplant is an understory shrub along edges and in gaps.
undetermined *TR LS — ? — S2

GENUS: **Siderone**

marthesia Cr.

Casearia (20)
sylvestris *DJ (81-SRNP-339) — ? — S2 — The hostplants are 2, 3 or 4 and range from saplings to mature trees. *Zuelania* records only on saplings.

Zuelania (20)
quidonia *DJ (81-SRNP-1045) — ? — S2

GENUS: **Zaretis**

itys Cr.

Ryanea (20)
speciosa LS — S1 — S1 — All hostplants are 2, 3 and 4 and range from saplings to mature forest trees, except Pi-peraceae, which are herbaceous. This species

Laetia (20)
procera LS — S1 — S1

Species	Hostplant & Locality	Egg & Larval Data		Bionomic Notes of Host and Butterfly
	Casearia (20)			feeds on a wide variety of hosts at La Selva, which also may be found to be the case in the Pacific drainage. Of interest is that Atlantic and Pacific drainage adults look very different; a detailed comparison of the early stages should provide an insight to whether or not the name *ellops* should be applied to the Pacific drainage insects.
	nitida LS	S1	S1	
	arborea LS	S1	S1	
	corymbosa *DJ (81-SRNP-272)	?	S1	
	arguta *DJ (81-SRNP-232)	?	S1	
	undetermined *JM CFDO	?	S	
	Piper (32)			
	arieianum *RM LS	?	S1	
GENUS: Consul				
fabius Dbldy.	*Piper* (32)			
	sancti-felicis	S1	S2	Hostplants are 2, 3 and 4. Early instars rest on frass chains, later instars rest in a tube.
	tuberculatum	S1	S2	
	undescribed species	?	S2	
	auritum *JM CVDO	?	S2	
	amalago *DJ (81-SRNP-600)	?	S2	
jansoni Salvin	*Piper* (32)			
	reticulatum *JM CVDO	?	S2	All records of this species are from solitary late instar larvae from hostplants growing along forest or riparian edges.
	undetermined CAR	?	S2	
	reticulatum *RM LS	?	S2	
GENUS: Hypna				
clytemnestra Cr.	*Croton* (18)			
	schiedeanus *RM LS	?	S2	Marquis reports this from a solitary late instar larva feeding on a sapling plant. The larva rests on frass chains.
GENUS: Memphis				
eurypyle	*Croton* (18)			
confusa Hall	*jalapensis* SJ, ELROD	S1	S1	Hostplant is 3 or riparian edges, ranging from

saplings to mature trees.

glycerium Dbldy.

Croton (18)
jalapensis ELROD, AT — S1 — S1

Hostplant is 3, ranging from saplings to mature trees. Early instars rest on frass chains, later roll a tube.

aieda Guer.-Men.

Acalypha (18)
garnieri SRNP — S1 — S1

Hostplant is 3 or 4, ranging from saplings to mature shrubs. Early instars make frass chains, later they roll a tube.

arginussa eubaena Boisd.

Croton (18)
undetermined SJ, VB — S1 — S2
undetermined AT — ? — S2
schiedeanus LS — ? — S2

Hostplants are 2, 3 or 4 and range from saplings to mature forest trees. Early instars make frass chains, later they roll a tube.

pithyusa Felder

Croton (18)
jalapensis AT, SJ — S1 — S2
schiedeanus *JM CVDO — ? — S?

Hostplants are 1, 2, 3 or 4 and range from saplings to mature forest trees. Early instars make frass chains, later they roll a tube.

beatrix Druce

Piper (32)
undetermined EST, CAR — ? — S2

This species is recorded from solitary late instar larvae feeding on all leaves. The hostplant is a semi-woody vine growing at the bases of large trees in the forest.

artacaena Hew.

Croton (18)
schiedeanus LS — S1 — S2
schiedeanus *JM CVDO — ? — S2

Hostplants are 3 or 4 but most commonly along riparian edges. Early instars make frass chains, later they make tubes.

oenomais Boisd.

Croton (18)
bilbergianus *AA (79-70, 79-101) — S — S3

Aiello reared these from Barro Colorado, Panama. There the hostplant occurs as a small tree in light gaps.

cleomestra Hew.

Piper (32)
undescribed species LS — ? — S2
xanthostachyum *RM LS — ? — S2

Hostplants are 2 or 4; one is an epiphytic vine, the other terrestrial. Early instars make frass chains, later they roll tubes.

Species	Hostplant & Locality	Egg & Larval Data	Bionomic Notes of Host and Butterfly
morvus boisduvalli Const.	*Persea* (23) undetermined *IC LS	? S2	Chacon records this species from a solitary late instar larva. The host was a mature tree along forest edge. Mature larvae roll tubes.
forreri G & S	*Ocotea* (23) *veraguensis* *DJ (81-SRP-939)	? S1	Hostplant is 2, 3 or 4. Early instars make frass chains, last instars roll tubes.

FAMILY: NYMPHALIDAE
SUBFAMILY: NYMPHALINAE

GENUS: Marpesia

Species	Hostplant & Locality	Egg & Larval Data	Bionomic Notes of Host and Butterfly
petreus Bates	*Ficus* (28) undetermined SRNP *goldmani* *DJ (81-SRNP-158a)	S1 S1 ?	Hostplants are 1, 2, 3 and 4 and usually large trees.
chiron Fab.	*Brosimum* (28) *alicastrum* *DJ (80-SRNP-113) *lactescens* *RM LS	? S2 S2	Both records are from late instar larvae on mature forest trees.
merops Boisd.	*Brosimum* (28) *lactescens* LS	? ?	This is a probable record based on mature larvae crawling down the tree trunk to pupate. The tree was isolated along forest edge. This record needs verification.

GENUS: Colobura

Species	Hostplant & Locality	Egg & Larval Data	Bionomic Notes of Host and Butterfly
dirce L.	*Cecropia* (28) various species: SRNP, MV, SV, TUR, SJ, LALT, VSM, CVDO, AT		All of my records have eggs laid in loose clusters of 10 to 30 eggs on saplings to mature trees. These have resulted in small clusters of

GENUS: **Historis**

odius Fab.

larvae that are semi-gregarious. J. Mallet reared "dirce" from La Selva and found gregarious masses of larvae composed of more than 30 individuals from emergent trees. There are striking differences in larval coloration suggesting that perhaps there are two species (*dirce* and *dirceoides*) as indicated in Sepp (1828).

Cecropia (28)			
peltata SRNP, AT, VSM	S1	S2	
undetermined LS, CAR, TUR	S1	S2	Hostplants are usually 3 or 4 depending on the habitat, ranging in size from saplings to mature trees. Early instars make frass chains, later they rest on the apical meristem.

acheronta Fab.

Cecropia (28)			
peltata SRNP, CVDO	S1	S1	Hostplants are usually saplings along edges. Larval behavior as for *odius*.

GENUS: **Smyrna**

blomfildia datis Fruh.

Urera (46)			
baccifera SRNP	?	S2	I have reared this from a solitary late instar larva. In SRNP the hostplant occurs as a riparian plant.

GENUS: **Pycina**

zamba zelys G & S

Urera (46)			
undetermined MV	S1	?	These records are from a number of oviposition records from mature plants along forest edge. I have not reared the larvae.
undetermined CAR	S1	?	

GENUS: **Tigridia**

acesta L.

Cecropia (28)	
undetermined LS, CAR	Females oviposit singly but tend to lay in loose

Species	Hostplant & Locality	Egg & Larval Data		Bionomic Notes of Host and Butterfly
	undetermined *JM Paurouma (28) aspera LS undetermined CAR			clusters of 3 to 8 eggs on the same leaf. Larvae are solitary or semi-gregarious and feed only on young leaves. Hostplants are always saplings and seedlings, and occur as 2, 3 or 4.
GENUS: Hamadryas				
februa Hubner	Dalechampia (18) scandens SRNP, AT	S1	S1	Hostplant is 2, 3 or 4 and ranges from juvenile to mature plants.
amphinome mexicana Lucas	Dalechampia (18) scandens SRNP	C	G1	Hostplant is 3 or 4; eggs in long chains.
guatemalena Bates	Dalechampia (18) scandens SRNP	S1	S1	Hostplant is 3 or 4 or vines ascending into the forest canopy.
laodamia saurites Fruh.	Dalechampia (18) undescribed species *JM LS	?	S2	Mallet reports this species from a solitary late instar larva. Hostplant was along forest edge ascending into the canopy.
iptheme Bates	Dalechampia (18) cissifolia *AA (78-66, 78-79)	S	S3	Aiello reports this from Panama where the hostplant occurs in open areas and along forest edges.
GENUS: Ectima				
rectifascia But. & Dru.	Dalechampia (18) undescribed species LS	S1	S3	Hostplants are 3 and 4 and are all juvenile plants.
GENUS: Eunica				
monima	Bursera (9)			

Species	Hostplant			Notes
modesta Bates	*simaruba* SRNP	S1	S3	Hostplant can be 1, 2, 3 or 4 and during outbreak years the larvae can defoliate entire trees.
mira G & S	*Mabea* (18)			
	occidentalis *KS-BCI	?	S5	Steiner reports that in Panama larvae are only found on male portions of the infloresence and not on leaves; plants are riparian. At La Selva I
	occidentalis LS	S1	S3-5	found that eggs are laid on fruiting trees and that first instars will feed on very new leaves; the plants occur in deep forest.
mygdonia Godart	*Mabea* (18)			
	occidentalis *KS-BCI	?	S5	Steiner reports this species as in *mira*.

GENUS: Dynamine

Species	Hostplant			Notes
salpensa Bates	*Dalechampia* (18) undescribed species LS	S1	S5	Hostplant is 3 or 4. Females oviposit only on developing flowers, larvae feed only on flower bracts and developing ovaries. Larvae will not eat leaves.
mylitta Cr.	*Dalechampia* (18) *scandens* SRNP, VSM	S1	S3-5	Hostplant is 3 or 4; larvae feed only on new leaves or flower parts.
glauce Bates	*Dalechampia* (18) *cissifolia* AT	S1	S3-5	Hostplant is 3 or riparian edge; larvae only feed on new leaves or flower parts.
hopi *albicola* Rober	*Dalechampia* (18) undescribed species LS	S1	?	Mallet records this as an oviposition record on flower buds.

GENUS: Temenis

Species	Hostplant			Notes
laothoe *libera* Fab.	*Serjania* (37)			
	paucidentata CVDO	S1	S2	Hostplants are 2, 3 and 4 and range from juvenile to mature plants. Females oviposit on damaged portions of leaves. Early instars make frass chains, later rest on leaf edges.
	undetermined LS	S1	S2	
	atrolineata *DHJ (81-SRNP-1092)	?	S2	
	Paullinia (37) undetermined *RM LS			

Species	Hostplant & Locality	Egg & Larval Data	Bionomic Notes of Host and Butterfly
GENUS: Epiphile			
adrasta Hew.	*Serjania* (37) undetermined MV *Cardiospermum* (35) undetermined SJ	S1 S2 S1 S2	Hostplants are 2 or 4 or as canopy vines and range from juvenile to mature plants. Early instars make frass chains, later instars rest on upperside of leaves.
orea plusios G & S	*Serjania* (37) undetermined CAR	S1 S2	Hostplants are 2, 3 or 4 or canopy vines. Early instars make frass chains; later instars rest on frass chains or upperside of leaves.
GENUS: Catonephele			
numilia esite Feld.	*Alchornea* (18) *costaricensis* LS	S1 S2	Hostplant is 3 and 4. Females oviposit on sapling sized plants. Early instars make frass chains, later instars rest on the uppersides of leaves.
orites Stichel	*Alchornea* (18) *costariensis* LS	S1 S2	Hostplants are 2, 3 and 4. Females oviposit on seedlings and saplings, usually within the seed shadow of a mature tree. Early instars make frass chains, later instars rest on upperside of leaves.
chromis godmani Stichel	*Alchornea* (18) *poasana* EST	S1 S?	This is an oviposition record where the female laid single eggs on sapling sized plants along forest edge. Larvae were not reared to adulthood.
nyctimus Wstwd.	*Veconcibea* (18) *pleistemona* *IC LS	? S2	Chacon records this from a solitary larva on a sapling sized tree along forest edge.

GENUS: Nessaea

aglaura Dbldy. & Hew.

Alchornea (18)

costaricensis LS	S1	S2	*Alchornea* is 2, 3 and 4; all seedlings. Early instars make frass chains, later instars rest on upperside of leaves. Marquis records this species from a solitary late-instar larva feeding on all leaves.

Plukenetia (18)

volubilis *RM LS	?	S2	

GENUS: Diaethria

eupepla G & S

Serjania (37)

undetermined LALT	S1	S2	Hostplants are 2, 3 and 4, and range from juveniles to canopy vines. Early instars make frass chains, later rest on leaves.

marchalli Guer.-Men.

Trema (44)

micrantha LS, CAR, VSM, SV	S1	S1	Hostplants are 2, 3, 4 and range from saplings to mature trees. Early instars make frass chains, later they rest on the underside of leaves.

GENUS: Callicore

pitheas Latr.

Serjania (37)

mexicana *AA (78-92) BCI	S	S1	Aiello states that early instar larvae skeletonize the young leaves, later instars are on all leaves. The hostplant is 3 and 4.

lyca
aerias G & S

Serjania or Paullinia (37)

undetermined SV, LS	S1	S1	Hostplants are 3 and 4, usually canopy or sub-canopy vines.

GENUS: Pyrrhogyra

edocla Dbldy. & Hew.

Serjania (37)

undetermined SV	?	S2	I reared this species from late-instar larvae on large woody vines occurring along forest and riparian edges. Larvae make frass chains.

crameri Aur.

Paullinia (37)

undetermined CVDO	S1	S1	Hostplant is 2, 3 and 4. Females oviposit only on newly emerging leaves. Larvae make frass chains.

Species	Hostplant & Locality	Egg & Larval Data	Bionomic Notes of Host and Butterfly
GENUS: Adelpha			
melanthe Bates	*Trema* (44)	S1	S2-4 All hostplants are 1, 2, 3 or 4 depending on the habitat and range from young to mature plants. Early instars make frass chains, later instars rest on leaves. Although all leaves are acceptable to larvae, they are usually found on old leaves.
	micrantha SRNP, VSM		
	Urera (46)		
	undetermined LS		
	undetermined CAR, VDS		
	Myriocarpa (46)		
	longipes LS		
	Cecropia (28)		
	undetermined MV, SV		
celerio Butler	*Urera* (46)	S1	S2 *Urera* is 3 and 4 in swampy areas that receive bright sunshine. Early instars make frass
	undetermined LS		
	Miconia (26)	?	S? chains, later instars rest on uppersides of leaves.
	argentea *JM CVDO		
iphicla *iphicleola* Bates	*Calicophyllum* (35)	?	S2 Janzen records this species from several late instar larvae feeding on all leaves. The hostplant is 3 and 4.
	candidissimum *DJ (79-SRNP-135)		
bassiloides Bates	*Ixora* (35)	?	S All records are from late instar larvae feeding
	nicaraguensis *RM LS	?	S on all leaves. Hostplants are found as 3 and 4.
	nicaraguensis *JM CVDO		
	Alibertia (35)	?	S
	edulis *DJ SRNP		
tracta Butler	"unknown genus" (35)	?	S2 Both records are from late instar larvae feeding
	undetermined *WH MV	?	S2 on all leaves of an unidentified woody shrub along forest edges.
	undetermined *IC PAT		
boeotia *boeotia* Felder	*Luehea* (41)	?	? No information as to larval feeding. The host
	seemannii *JM CVDO		

Taxon / Hostplant		
heracleta Felder		
Vitex (47)		
cooperi LS	S1	S1
Piper (32)		
arieianum *RM LS	?	S1
boreas		
tizona Fruh.		
Chomelia (35)		
bispinosa VDS	S1	S?
Satyria (16)		
undetermined *RM LS	?	S?
zalmona		
sophax G & S		
Sabicea (35)		
aspera CAR	S1	S1
leucophthalma		
mephestopheles But.		
"Unknown genus" (35)		
undetermined SV, CAR	S2	S2
cocala		
lorzae Boisd.		
Pentagonia (35)		
macrophylla LS	S2	S2
Psychotria (35)		
undetermined *RM LS	?	S4
Calycophyllum (35)		
candidissimum *DJ (81-SRNP-740)	?	S?

commonly occurs as all categories in Corcovado but no information on where early stages are likely to occur.

Vitex is in my experience the common host at La Selva and is 3 and 4, usually from saplings to mature trees. *Piper* record is from a late instar larva feeding on all leaves in light gap. Larvae rest on frass chains. These records represent quite a diverse set of hostplants from the same locality.

I have not succeeded in rearing this species to adulthood. Early instars on *Chomelia* feed on new leaves and make frass chains. *Chomelia* occurs as 3 and 4. Marquis records this species from a solitary late instar larva; *Satyria* is an epiphyte. This is an unusual record for the family Nymphalidae.

Hostplants are along roadsides, riparian edges in bright sunshine. Early instars make frass chains, later instars rest on leaves.

Hostplants are 2, 3 and 4 depending on the habitat and range from seedlings to saplings. Early instars make frass chains, later they rest on upperside of leaves.

Pentagonia is 2, 3, 4 and is either seedling or sapling sized; *Psychotria* is sapling-2. Females oviposit on damaged portions of old leaves. Larvae feed on old leaves in all plants and make frass chains.

Species	Hostplant & Locality	Egg & Larval Data		Bionomic Notes of Host and Butterfly
cytherea marcia Fruh.	Sabicea (35)			
	villosa LS, CAR, CVDO	S1	S1	Hostplants are 3 and 4 in bright sunshine. All instars rest on frass chains. Mallet reared this species from the same hostplant in Corcovado.
fessonia Hew.	Randia (35)			
	echinocarpa *DJ (79-SRNP-216)	?	S2	These records are from solitary late instar larvae. Hostplants are 3 and 4.
	karstenii *DJ (81-SRNP-725)	?	S2	
demialba Butler	Rondeletia (35)			
	undescribed species *WH MV	?	S3	This record is from a solitary late instar larva; hostplant was 3.
GENUS: **Hypanartia**				
lethe Fab.	Phenax (46)			
	undetermined SJ	S2	S1	Hostplants are 1 and 3. Phenax is an herbaceous plant in open areas, Trema is a secondary succession tree. On Phenax the larva forms a cup from one leaf with silk and rests and eventually pupates in this silk lined cup.
	Trema (44)			
	micrantha *DJ (81-SRNP-296)	?	S	
GENUS: **Siproeta**				
stelenes biplagiata Fruh.	Blechum (1)			
	pyramidatum *DJ (81-SRNP-71)	?	S2	Hostplants are all 1.
	undetermined CAR			
GENUS: **Chlosyne**				
hyperia Fab.	Melanthera (13)			
	aspera SRNP	?	S2	Hostplant is 1.

Species	Hostplant			Notes
gaudialis Bates	*Justicia* (1) undetermined	?	S2	Hostplant is 3, 4 ranging from seedling to mature plants.
narva bonplandi Latr.	*Amaranthus* (2) undetermined LS	C?	G2	Hostplant is 2, 3 and 4 from seedling to mature plants.
lacinia Geyer	*Clibadium* (13) undetermined *RM LS	C?	G2	Reported from a mass of late instar larvae on an open area plant.
melanarge Bates	*Aphelandra* (1) deppiana SRNP	C?	G2	Hostplant is 2, 3 and 4 ranging from juvenile to mature plants.
GENUS: Eresia				
coela Druce	*Justicia* (1) undetermined LS / *Herpetacanthus* (1) panamensis *LEG LS	C / ?	G / G	Hostplants are 2, 3 and 4. *Justicia* are usually seedlings. I have not reared this species to adulthood on *Justicia*.
GENUS: Castilia				
ofella Hew.	*Justicia* (1) comaeta LS / *Aphelandra* (1) storkesi *JM CVDO	C / ?	G2 / G	Hostplants are 2, 3, 4 ranging from juvenile to mature plants. Eggs in clusters of 20 to 40.
myia Hew.	*Justicia* (1) undetermined LS	C	G?	This record is from a single batch of 10 larvae feeding on a mature plant along forest edge.
eranites Hew.	*Justicia* (1) undetermined LS	C	G	I record this from several oviposition records all on seedling plants in open areas. First instar larvae feed on new leaves, later instars feed on all leaves. I have not reared this species to adulthood.

Species	Hostplant & Locality	Egg & Larval Data		Bionomic Notes of Host and Butterfly
GENUS: Anthanassa				
ptolyca Bates	*Justicia* (1) undetermined **AA (80-65) BCI	?	?	Aiello records this species from several late instar larvae feeding on all leaves. The host occurs along roadsides as an herbaceous weed.
GENUS: Tegosa				
anieta Hew.	*Vernonia* (13) undetermined VDS	C	G2	Hostplants are 3 or riparian edges and range from juvenile to mature plants.
GENUS: Euptoeita				
hegesia hoffmani Comstock	*Turnera* (43) *ulmifolia* SRNP, CVDO	S2	S1	Hostplants are 1, either juvenile or mature plants.

FAMILY: NYMPHALIDAE
SUBFAMILY: HELICONIINAE

The bulk of the pertinent Costa Rican hostplant records has been reported by Benson, et. al. (1978) and the reader is referred to that paper. The records presented here complete their picture.

GENUS: Dryadula				
phaetusa L.	*Passiflora* (31) *talamancensis* *JM CVDO	S	S2	Mallet records this species from late instar larvae on host growing in open areas of bright sunshine.
GENUS: Eueides				
vibilia	*Passiflora* (31)			

vialis Stichel	*pittieri* *JM CVDO	?	G4	This species is reported from a solitary cluster of larvae on a host in the forest.
procula *vulgiformis* But. & Dru.	*Erblichia* (43) *odorata* *DJ (79-SRNP-408)	?	G	Janzen reports that larvae make holes in the leaf as early instars and later feed at the leaf margins. The hostplant is a forest tree (see Janzen, 1983).

SUBFAMILY: ACRAEINAE

GENUS: **Actinote**

leucomelas Bates	*Mikania* (13) undetermined SV, MV, CAR	C	G1	Hostplant is 1, 2, 3 and 4.
lapitha Staud.	*Mikania* (13) *riparia* CVDO	?	G2	Hostplant is 1 as a scandent semi-woody vine.

SUBFAMILY: DANAINAE

GENUS: **Anetia**

thirza *insignis* Salvin	*"genus?"* (5) undetermined COP	S1	?	This represents an oviposition record.

GENUS: **Lycorea**

cleobaea *atergatis* Dist.	*Carica* (12) *papaya* LS, SJ, ELROD	S1	S2	Hostplants are 2, 3, 4 and range from juvenile to mature forest trees. There is variation among hosts as to what plant fraction the larva will eat. Larvae feeding on Caricaceae cut the main and accessory veins of the leaf and then feed on the leaf portion distal to stem; presumably to avoid secondary compounds.
	Jacaratia (12) *dolichaula* LS	S1	S2	
	Ficus (26) undetermined *WH MV	?	S3	
	undetermined *DJ (79-SRNP-113)	?	S3	
	Matalea (5) *quirosii* *DJ (79-SRNP-131)	?	S	
	Asclepias (5) *curassavica* *WH MV	?	S	

Species	Hostplant & Locality	Egg & Larval Data		Bionomic Notes of Host and Butterfly
iliore albescens Distant	*Ficus* (28) tuerckheimii *WH MV	?	S3	Haber reports this from a solitary late instar larva feeding on the stump sprouts of the hostplant growing in an open pasture.

SUBFAMILY: ITHOMIINAE

The bulk of Costa Rican hostplant records for the Ithomiinae may be found in Haber (1978). The following records are additions or new records to his list or records gathered by other workers. In addition in the present list I have included data pertinent to eggs, larvae and adults.

GENUS: Melinaea

Species	Hostplant & Locality	Egg & Larval Data		Bionomic Notes of Host and Butterfly
lilis imitata Bates	*Markea* (40) neurantha LS, CAR	S1	S1	Hostplant is an epiphyte, females oviposit on plants occurring as 2, 3, 4 and range from seedling to mature plants. Early instars cut leaf veins before feeding on tissues distal to the stem.
scylax Bates	*Juanuloa* (40) mexicana *LEG	S1	S1	In the insectary, females of Costa Rica stock preferentially oviposited on this plant (Mexican origin) although *Markea* and *Solandra* were present, and both are used by *lilis imitata* in the insectary. All hostplants are epiphytic.

GENUS: Mechanitis

Species	Hostplant & Locality	Egg & Larval Data		Bionomic Notes of Host and Butterfly
polymnia isthmia Bates	*Solanum* (40) lancaefolium *LEG LS	C	G2	Hostplants are 3 and 4 and range from seedlings to mature vines.
	lancaefolium *RM LS	C	G2	
	torvum *FGS UCR	C	G2	
menapis saturata G & S	*Solanum* (40) torvum CAR	C	G2	Hostplants are 3 or riparian edges.
	torvum *FGS UCR	C	G2	

GENUS: Ithomia

patilla Hew.

Witheringia (40)
solanacea *FGS UCR — S1 S2 — Hostplants are 3 and 4.
undetermined species *LEG SV — S1 S2

diasa
hippocrennis But. & Dru.

Lycianthes (40)
heteroclita *LEG LS — S1 S2 — Hostplants are 3 and 4.

heraldica Bates

Acnistus (40)
arborescens SV, SJ, UCR, PAT — S1 S2 — Hostplants are 1, 3 and 4 and may be young or mature plants.

Witheringia (40)
undetermined species *LEG SV,LS — S1 S2
Capsicum ? (40)

celemia

plaginota But. & Dru.

undetermined species *LEG RCN — S1 S2 — Hostplant occurs as an understory forest shrub and is acceptable as young and mature plants. Probably a *Witheringia* (S. Knap, pers. comm.).

xenos Bates

Acnistus (40)
arborescens *FGS UCR — S1 S2 — Hostplants are 2, 3 and 4.

GENUS: Ceratinia

tutia
dorilla Bates

Solanum (40)
nudum *LEG RCN — S1 S2 — Hostplants are forest understory shrubs and usually occur in heavy second growth vegetation.
nudum *JM CVDO — S1 S2

GENUS: Dircenna

klugi Geyer

Solanum (40) *all FGS
umbellatum UCR — S1 S2 — Stiles records all of these species from the same locality. All hostplants are 2, 3, 4 provided open sunshine during a part of the day.
torvum UCR — S1 S2
lanceolatum UCR — S1 S2
ochraceo-ferruginium — S1 S2

Species	Hostplant & Locality	Egg & Larval Data		Bionomic Notes of Host and Butterfly
euchytma Feld.	*Solanum* (40) *ochraceo-ferruginum* *LEG LS	S1	S3	Hostplants are 3 and riparian edges.
GENUS: Godyris				
zygia G & S	*Cestrum* (40) *nocturnum* *LEG SV	S1	S2	Hostplants are understory shrubs and range from juvenile to mature plants.
GENUS: Hyalyris				
excelsa decumena G & S	*Solanum* (40) *lancaefolium* SJ, CAR, VDS	S1	S1	Hostplants are 2, 3 or 4 and usually seedling or sapling plants.
GENUS: Hypothyris				
lycaste callispila Bates	*Solanum* (40) *umbellatum* *FGS UCR *ochraceo-ferruginium*	S1	S2	No data on hostplant habitat.
euclea valore Haensch	*Solanum* (40) *umbellatum* *FGS UCR	S1	S?	No data on hostplant habitat.
GENUS: Episcada				
salvinia opleri Lamas	*Solanum* (40) "new species" *LEG SV *nudum* IFGS UCR	C C	G2 G2	Hostplants are all second growth shrubs.
GENUS: Pteronymia				
agalla obscurata Fab.	*Solanum* (40) *brenesii* *LEG SV, RCN	S1	S?	No data on hostplant habitat.

artena Hew.

Lycianthes (40) undetermined species *LEG *Solanum* (40) *confirme* "new species" *JM	? ? ?	S? S2 S2	Gilbert reports this from several eggs on old leaves. No data on hostplant habitat. Mallet reports this from *Solanum* which are all second growth or forest understory shrubs.
lonera But. & Dru. *Cyphomandra* (40) *costaricensis* *LEG SV	S1	S1	Hostplant is 3 and 4. Females oviposit on mature plants.

SUBFAMILY: MORPHINAE

GENUS: Antirrhea

pterocopha G & S *Calypterogyne* (30) undetermined CAR	?	S4	Hostplants are solitary, growing in dense shade, usually at the base of a large tree. Larvae feed on leaves that are covered in epiphylls.
miltiades Fab. *Geonoma* (30) *longivaginata* *RM LS	?	S4	Marquis reports this from a solitary late instar larva from a plant growing in deep shade.

GENUS: Caerois

gerdrudtus Stich. *Socratea* (30) undetermined *IC LS	?	S2	Chacon reports this from a solitary late instar larvae feeding on a large tree growing in a swamp.

GENUS: Morpho

amathonte Dey. *Pterocarpus* (19) *officinalis* CVDO	?	S2	I report this from a solitary late instar larva feeding on a sapling in a swamp. The larva fed nocturnally.
granadensis *polybapta* Butler *Machaerium* (19) *seemani*	S?	S2	I report this from solitary larvae feeding on

Species	Hostplant & Locality	Egg & Larval Data		Bionomic Notes of Host and Butterfly
peleides Esper				seedling and sapling sized plants. Females lay on this plant when confined.
	Machaerium (19)			
	seemanii LS, CVDO, CAR, VSM	S	S2	Hostplants are all 2, 3, 4 and range from seedlings to large forest trees. Larvae are nocturnal feeders and usually crawl off the host leaves while not feeding.
	undetermined LSALT	S?	S2	
	undetermined VDS	S?	S2	
	biovulatum *DJ (81-SRNP-711)	S?	S2	
	Mucuna (19)		S2	
	mutisiana **confined female MV, SV			
	Dalbergia (19)	S?	S2	
	retusa *DJ (81-SRNP-226)			
	Pterocarpus (19)	?	?	
	rohrii **AA (80-16) BCI			

SUBFAMILY: BRASSOLINAE

GENUS: Dynastor

Species	Hostplant & Locality	Egg & Larval Data		Bionomic Notes of Host and Butterfly
darius *stygianus* Butler				
	Aechmea (8)			
	magdalenae LS	S1	S2	Hostplants are 2, 3, 4 and in swampy areas if terrestrial. The undetermined record is an epiphyte. Larvae rest in the middle of the leaf blade when not feeding.
	undetermined LS	?	S2	
	Bromelia (8)			
	pinguin *DJ (82-SRNP-1308)	?	S2	

GENUS: Opsiphanes

Species	Hostplant & Locality	Egg & Larval Data		Bionomic Notes of Host and Butterfly
tamarindii *sikyon* Fruh.				
	Heliconia (21)			
	various species LS, CVDO, SJ	S1	S2	Hostplants can be 1, 2, 3 or 4.
cassina *fabricii* Boisd.				
	Acrocomia (30)			
	vinifera SRNP	S1	S2	Hostplants are 1 or 3 and range from juvenile to large trees.
	Cocos (30)			
	nucifera CVDO	S1	S2	

staudingeri G & S	*Chusquea* (34) undetermined *IC PAT	?	S2	Chacon reports this species from late instar larvae which feed nocturnally.
bogatanus Distant	"palm" (30) undetermined *RC VDS	?	S2	Cubero reports this from larvae feeding on juvenile plants growing in the forest.

GENUS: Eryphanis

polyxena lycomedon Felder	"exotic bamboo" (34) *RC	S	S2	Cubero reports this from a confined female. Larvae feed nocturnally.

GENUS: Caligo

****NOTE:** It is common in the hostplant literature to record *Caligo* from *Musa*. However this certainly represents a radiation onto an introduced plant; *Musa* is native to the Old World. In my rearing studies of *Caligo* I have found that any species of *Heliconia* will serve as a hostplant and a stimulus to oviposit, both in the field and in the insectary.

memnon Fedler	*Heliconia* (21) various species SJ, SV, AT, CVDO	See Comments		Hostplants are 2, 3 or 4 and range from juvenile to mature plants. Females oviposit small clusters of eggs (2-15) and then will lay several clusters on the same plant. All leaves are acceptable to all instars.
eurilochus sulanus Fruh.	*Heliconia* (21) various species CAR, CVDO, LS, SV, LALT	C1	G2	Hostplants are 2, 3, 4 and range from juvenile to mature plants. Larvae are gregarious and aggregations may contain all instars without cannibalism.
atreus Kollar	*Heliconia* (21) various species CAR, LS, CVDO	C2	G2	Hostplants are 2, 3, 4 and range from juvenile to mature plants. Chacon reports this record from a solitary late instar larva on old leaves. Usually larvae are in small aggregations where all instars may be present without cannibalism.
	Asterogyne (30) *marshiana* *IC LS	?	S	

Species	Hostplant & Locality	Egg & Larval Data		Bionomic Notes of Host and Butterfly
illioneus Kollar	*Heliconia* (21) various species LS	C2	G2	Hostplants are 2, 3, 4 and may range from juvenile to mature plants. Larvae are gregarious and may be present in all instars without cannibalism.
SUBFAMILY: SATYRINAE				
GENUS: Dulcedo				
polita Hew.	*Geonoma* (30) undetermined LS	S1	S1	Hostplants are all seedlings occurring in well shaded swampy areas.
	Euterpe (30) undetermined LS	S1	S1	
GENUS: Pierella				
luna Fab.	*Heliconia* (21) latispatha CVDO	S2	S2	Hostplants are all seedlings occurring in well shaded light gaps.
	Calathea (25) marantifolia *JM CVDO	?	S2	
helvetia incanescens G & S	*Heliconia* (21) various species LS, TUR	S2	S2	Hostplants are all 2, 3, 4 and are seedlings except for *Panicum*.
	Asterogyne (30) undetermined LS	S2	S2	
	Calathea (25) undetermined LS	S2	S2	
	Panicum (33) undetermined *MCS CVDO			
GENUS: Cyllopsis				
philodice G & S	*Swallenochloa* (34)			

Species	Hostplant			Notes
argentella But. & Dru.	undetermined COP, CDM	S1	S3	Hostplants occur in dense stands in open areas at high elevations.
	Chusquea (34) undetermined COP, PAT	C?	*G2	Hostplants occur as dense stands along riparian edges or forest edges. Early instars are gregarious, later instars appear to be solitary (I have only lab reared them in later stages). Eggs are laid on young plants with abundant new growth.
GENUS: Oressinoma *typhla* West. & Hew.	*Cyperus* (15) *lazulae* BLH, CAR	S2	S1	Hostplants occur in open areas usually associated with swampy or riparian situations.
GENUS: Taygetis *andromeda* Cr.	*Olyra* (33) *latifolia* *DJ (81-SRNP-946)	?	S2	Janzen reports this species from solitary larvae feeding on hostplants growing along forest edges.
GENUS: Euptychia *insolata* But. & Dru.	*Neckeropsis* (29) *undulata* *MCS CVDO	S1	S2	Hostplant is an epiphytic moss on tree trunks in well shaded rainforest habitats. This is a highly unusual host record for any butterfly family.
jesia Butler	*Selaginella* (38) *horizontalis* *MCS LS, CVDO, SV undetermined species ELROD undetermined CAR	S1 S1 S1	S2 S2 S2	Hostplants are 2, 3 and 4.
westwoodi Butler	*Selaginella* (38) *arthriticum* *MCS LS, SV, CVDO, AT	S1	S2	Hostplants are 2, 3 and 4.

Species	Hostplant & Locality	Egg & Larval Data		Bionomic Notes of Host and Butterfly
molina Hub	*Selaginella* (38)			
	arthriticum *MCS SV	S1	S2	Hostplants are 2, 3 and 4.
	undetermined CAR	S1	S2	
GENUS: Chloreuptychia				
arnaea Fab.	*Eleusine* (33)			
	undetermined *MCS SV, CVDO	S1	S2	Hostplants occur in isolated clumps in light gaps and at bases of trees.
	Oplismenus (33)			
	undetermined *MCS AT	S1	S2	
	Ichnanthus (33)			
	undetermined *MCS LS	S1	S2	
	undetermined CAR	S1	S2	
GENUS: Cissia				
usitata Butler	*Eleusine* (33)			
	indica *MCS LS, CVDO	S2	S2	Hostplants occur along sunny edges and light gaps.
thenis Butler	"various grasses" (33)			
	undetermined *MCS AT	S2	S2	Hostplant occurs in small clumps in open forest.
confusa Staud.	*Panicum* (33)			
	undetermined *MCS CVDO	S2	S2	All hostplants occur as isolated clumps (grass) or seedlings (palms and *Calathea*) on the shady forest floor.
	undetermined CAR	S2	S2	
	Euterpe (30)			
	undetermined *MCS LS CVDO	S2	S2	
	Geonoma (30)			
	congesta LS, CAR	S2	S2	
	Calathea (26)			
	undetermined LS	S2	S2	

Species	Hostplant			Notes
labe Butler	"grasses" (33) undetermined *MCS LS			The eggs are deposited singly off the hostplants, usually on nearby dead vegetation. The host occurs in lush, tall clumps in large light gaps.
palladia Butler	"various grasses" (33) greenhouse data *MCS LS			In captivity, eggs are laid singly. All leaves of various grasses were acceptable to all instars.
pseudoconfusa S, D & E	*Panicum* (33) undetermined LS, CVDO, SV	S2	S2	Hostplants occur in isolated clumps in shady forest.
	"grass" (33) undetermined CAR	?		
gomezi S, D & E	"grass" (33) undetermined *MCS CVDO	?	S2	This is recorded from a solitary late instar larva feeding on a grass growing along forest edge.
libye L.	*Panicum* (33) maximum SRNP, AT	S2	S2	Hostplants are 3 and 4 provided there is direct sunshine at some time of the day.
	"various grasses" (33) undetermined *MCS LS, CVDO, SV	S2	S2	
renata Cr.	"various grasses" (33) undetermined *MCS AT, CVDO, SV	S	S2	Female oviposits off the hostplant on nearby vegetation and litter. Hostplants occur in very open forest or edges.
hesione Sulzer	*Eleusine* (33) various species *MCS LS, CVDO, SV	S2	S2	Hostplants occur as isolated clumps in open areas or along forest edges.
metaluca Boisd.	"grass" (33) undetermined *MCS LS, CVDO, SV	S2	S2	Hostplants occur in isolated clumps in the forest or along forest edges.
hermes Fab.	*Eleusine* (33) undetermined *MCS AT, CVDO	S2	S2	Hostplant almost always in open sunny areas, usually second growth, occasionally within the forest shade.
	Panicum (33) undetermined *MCS SV, LS	S2	S2	

Species	Hostplant & Locality	Egg & Larval Data		Bionomic Notes of Host and Butterfly
calixta Butler	*Laparus* (15) lazulae BLH, CAR	S2	S2	Hostplants occur in wet open areas along roadsides and trails, or riparian edges.
	"grass" (33) undetermined CAR	S2	S2	
polyphemus Butler	*Chusquea* (34) undetermined *IC PAT	S2	S2	Chacon reports this species from late instar larvae feeding on a dense stand of hostplant along forest edges. The larvae feed nocturnally.
GENUS: **Megeuptychia**				
antonoe Cr.	*Calathea* (25) lutea *JM CVDO *Cyclanthus* (14) undetermined LS	C	G2	Mallet reports this species from seedlings occurring in deep forest or along forest edges. My record is an oviposition as seen with binoculars while I was in the forest canopy.
GENUS: **Dioriste**				
cothonides GRS.-SMT.	*Chusquea* (34) undetermined COP, PAT	C	G2	Hostplants occur as dense thickets along forest and riparian edges. Early instars are gregarious, later instars are solitary. The larvae feed nocturnally.
GENUS: **Eretris**				
suzannae DeVr.	*Chusquea* (34) undetermined BLH	S1	S1	Hostplants occur as dense thickets along forest and riparian edges. The egg is deposited on the terminal spine of the leaf.

GENUS: **Pedaliodes**

perperna Hew.

Rhipidocladum (34) *maxonii* EST	S1	S1	Hostplants occur in isolated, juvenile clumps on the forest floor in old light gaps.

ereiba
cremera G & S

Chusquea (34) undetermined COP	S1	?	This is reported as an oviposition record only; larvae were not reared past first instar. Females lay eggs singly in the axils of the whorled leaves near the main stem.

GENUS: **Catargynnis**

rogersi G & S

Chusquea (34) undetermined BLH, COP, CAR	S2	?	Hostplants occur in dense stands in shady areas in the forest or edges. Females lay eggs in leaf axils; larvae not reared.

Invited Paper

Enzyme Electrophoresis and Interspecific Hybridization in Pieridae (Lepidoptera)

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Abstract. Sterility and incompatibility levels found in crosses of 12 Lepidoptera species (family Pieridae) were compared with differences between electrophoretic enzymatic patterns characteristic of the respective species (Geiger, 1978, 1981). Good agreement was found when different subgenera and genera were crossed while considerable disagreement prevailed at the subspecies and species levels. Inadequate estimates of low level taxa divergency, uneven development of reproductive isolating mechanisms and limitations of the scope of the electrophoretic approach are discussed as possible reasons for the observed discrepancies.

Key words: enzyme electrophoresis, hybrid sterility, interspecific crossings, taxonomical levels, Pieridae, Lepidoptera.

Introduction

Electrophoretic studies of enzymatic similarity are used increasingly to trace genetic relationships among taxa and to make phylogenetic interpretations. Indeed, Bullini (1983) referred to the technique as a revolution in taxonomy, or at the least a transformation phase of this discipline leading to a better comprehension of taxonomy as well as evolutionary processes. In the Lepidoptera, studies of populations, subspecies, sibling species and species complexes, and whole families have already been made, an oversight of Bullini (1983). Using diurnal Lepidoptera, Geiger (1978, 1981, 1984) carried out an extensive study on variations of 20 isoenzymes in 24 European species representing four subfamilies of the family Pieridae, and found good agreement between the coefficient of their enzymatic similarity, Nei's I value, and their systematic position and phylogenetic relationships.

Hybridization among 13 of the 24 Pierid species studied by Geiger were carried out at the biological laboratory in Zagreb for many years (Lorković, 1928, 1969, 1978). In combination with Geiger's data, this largely unpublished work has acquired new significance. Therefore some selected data will be presented here. The degree of relationship among the 12 *Pieris* species emerging from these hybridization experiments will be

compared with those derived from the enzyme studies of Geiger. A list of the primary works on enzyme genetics by Ayala, Nei, Lewontin and other authorities can be found referenced in the papers cited herein. No general discussion is made here of views on speciation, microevolution and phylogeny unless they are directly related to the subject in question.

Methods and Material

a) Crossing methods

Crosses were made using laboratory bred specimens derived from wild-inseminated females. Males were occasionally replaced with wild specimens to avoid inbreeding depression (see Oliver, 1981).

As the studied taxa, with two exceptions, were sexually isolated, interspecific crossings would naturally occur only exceptionally. Therefore, three artificial original crossing techniques were necessary:

(1) **natural pairing,** in which the pair designed for crossing was placed in a glass vessel together with an inactive male belonging to the species of the female. Pheromones released by this male could stimulate the female to accept the foreign male. In Pieridae, as with most other butterflies, it is usually the female which is able to distinguish between homospecific and heterospecific males, so that by such method mating may take place quickly without intervention from the breeder.

(2) Since Pieridae are too delicate for the rather rough hand-pairing, reintroduced by Clarke (1956), the **forceps-hand pairing** method (Lorković, 1947, 1953) was used where applicable. In *Colias*, the uncus and valvae of the male are too short for manipulation, even with the finest of forceps, thus making this method impracticable.

(3) Therefore the original **gynanaesthetic method** (Lorković in Friedrich, 1975, 1982, 1983) was used, in which the anaesthetized female is held with a pair of forceps by her folded wings and presented to the male in a cage. The male then grasps the genital part of the female abdomen with his uncus and valvae.

Rearing took place in the laboratory of the Biological Institute in Zagreb, in a room on the sunny side, with temperatures between 20°C and 30°C in summer with 70% R.H. and 50% R.H. in winter. Egg-laying and rearing of the young larvae, up to the 4th instar, took place on potted plants. Later food plants with stems in water were used. The cages employed were 25 cm cubes covered with fine nylon.

b) Material, Species & Sources

Species	Origin
Pieris rapae (Linneus, 1758)	Zagreb, Croatia, Yugoslavia
P. mannii (Mayer, 1851)	Adriatic coast, Plitvicka jezera, Zagreb (Croatia), St. Martin Vesubie (France, 1936)
P. ergane (Geyer, 1828)	Adriatic coast, Zagreb, Julian Alps
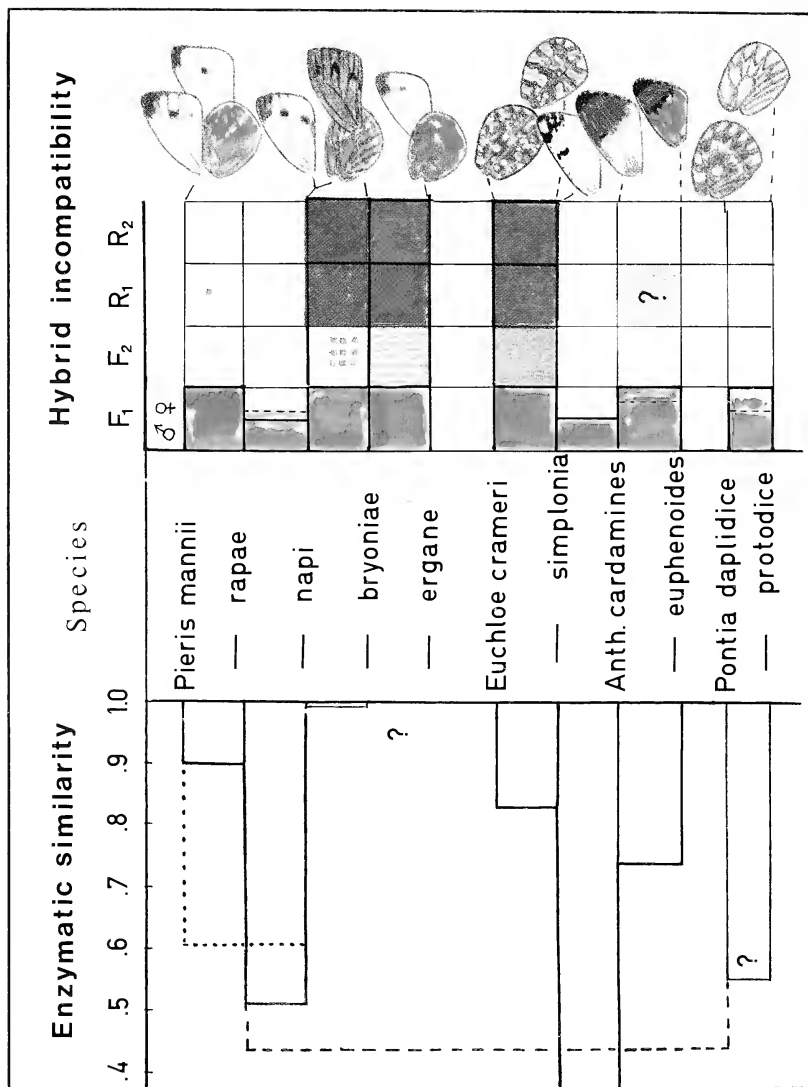
Plate I.

Plate II.
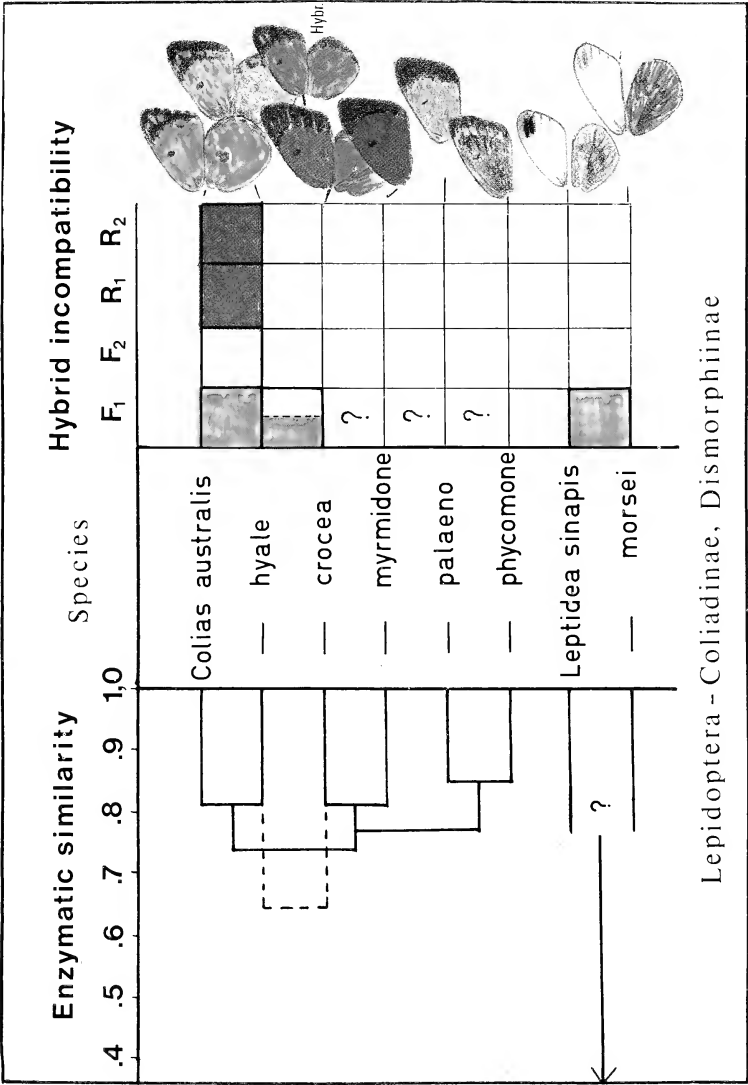
P. napi (Linneus, 1758)	Zagreb, Adriatic coast, Julian Alps; England; Cantabria Mts., Sierra de Gredos (Spain, 1972, Eitschberger)
P. bryoniae (Linneus, 1758)	Slovenian Alps, Austrian Alps, Bad Vöslau (Vienna); Les Mées, Les Fonds (Basses Alpes) (Descimon); Zermatt (Penninian Alps, 1964)
P. (pseudorapae) balcana (Lorković, 1968)	Treska gorge, Negorci (Macedonia), Zelengora (SE Bosnia), Slunj, Plitvicka jezera (Croatia)
P. oleracea (Harris, 1829)	New Hampshire, USA (S. R. Bowden)
Pontia daplidice (Linneus, 1758)	Zagreb
P. protodice (Boisduval, 18)	Chicago (USA)
Euchloe simplonia (Boisduval, 1828, nec **simplonia** Freyer, 1829)	Zermatt (Switzerland, 1964; W. Back, 1979)
E. ausonia graeca (Staudinger, 1869)	Dalmatia (Croatia), Treska gorge (Macedonia)
E. crameri (Butler, 1869)	Nice (France, 1936); Les Mées (Basses Alps), W. Back, 1979
Anthocharis cardamines (Linneus, 1758)	Zagreb, Podsused, Pustodol
A. euphenoides (Staudinger, 1869)	Nice (France, 1936)
C. alfacariensis Berger, 1948, (=**australis** Verity, 1911)	Zagreb, Ika; Véseley (Dijon, France)
C. crocea (Geoffroy in Fourcroy, 1785)	Zagreb

Additonal information was also obtained from crossings of the European *Pieris napi* and the Japanese *P. melete* (Ménétriés, 1857), *P. nesis* Fruhstorfer, 1908 (=*japonica* Shirozu, 1952) and *P. dulcinea pseudonapi* Verity, 1911; of *P. rapae rapae* L. with *P. rapae crucivora* (Boisduval, 1836); and of *P. marginalis* (Scudder, 1861), *P. virginiensis* (Edwards, 1870) and *P. oleracea* (Harris, 1829) from North America, the latter kindly supplied by S. R. Bowden. The data on these crosses are not included in the present paper, except those involving *P. oleracea*, because of the lack of correlative enzymatic data.

A survey of common features involving interspecific hybrids

The purpose of this work is to compare two criteria for Pierid genetic relationships. One of these, enzymatic, is relatively straightforward and quantifiable while the other, sterility, is complex. As a measure of genetic incompatibility, sterility is a consequence of a number of developmental barriers contributing unequally to the ultimate failure of hybrid reproduction. The term "sterility" is used here in the broadest sense to denote incapacity of reproduction irrespective of the exact mechanism of hybrid inviability (e.g., failure of gametogenesis, zygote lethality, loss of fecundity, etc.). A "sterility" grading system was therefore established to score

for developmental success. Usefulness of the system requires a knowledge of the degree of incomplete development. Some typical hybrid characteristics are described below.

First, it will be recalled that in Lepidoptera disturbance of fertility generally occurs more frequently in females than in males because the females are the heterogametic sex (i.e., having a pair of unequal sex-determining chromosomes, XY or XO) which, in agreement with Haldane's rule, renders the females more affected than males in crosses. The reader can refer to the following works for further discussion on the properties of sterility in interspecific hybridization: Bytinski-Salz (1930, 1934), Federley (1911-1953, for bibliography see Suomalainen, 1952), Clarke and Sheppard (1953, 1955, 1964, etc.), Remington (1956, 1958, 1960, 1968), Bowden (1956) and most recently Oliver (1977, 1979a, b) (for bibliography see Suomalainen, 1952).

1. The least obvious genetic disturbance is a shortened development time of hybrid females, known as protogyny (eclosing of females before males). Protogyny does not involve the sterility of an individual hybrid. It is merely a disadvantage to the population as a whole, but may however favor back crosses.

2. A more serious sterility producing effect encountered in females is a physiological disturbance of diapausing female larvae or pupae consisting in their inability to terminate their diapause period. This leads to a lack of viable females in the spring brood and results in abnormal sex ratios in the adult population. When females develop directly (without diapause) they are fertile at least to a degree.

3. Further in the descending order of fertility, female sterility is encountered preventing the appearance of an F_2. The near absence of the F_2 generation is the main characteristic of the hybrids studied here, excepting hybrids in the genus *Euchloe*. At this level of sterility, reproduction is limited to the male sex in backcrosses (R_1).

4. At the fourth level, both sexes are sterile in the F_1 and the females show deformation, usually expressed as crippled wings, while the males are more viable and better developed.

5. The lowest fertility was found in intergeneric matings such as *Pontia* x *Pieris* which are characterized by a high egg-laying rate and egg fertility while embryonic development is 95% incomplete. With this case, the fertility limit for Lepidoptera appears to be reached.

Data on egg laying, egg embryonic development and rate of larval hatchability are given here only for the last mentioned crosses of *Pontia* x *Pieris*. In the other crosses the role played by the egg development is reflected in part in the numbers and the degree of sterility of F_1, F_2 and R generations. A more thorough analyses is beyond the scope of this paper.

Plates I and II summarize relationships between the taxa discussed here based on comparison of enzyme electrophoresis and hybrid sterility analysis. The left hand column presents dendrograms based on enzymatic similarity, $\bar{I}$ (Geiger, 1981). In the remainder of this paper enzyme relationships are expressed as difference (EDf) in order to directly compare values with sterility grades. The right column gives sterility values for F_1, F_2, and two backcross (R_1 and R_2) crosses. A full colored square denotes normal development of adult males and females. Absence or numerical deficiency of either sex (usually the female) is indicated by a line dividing the square into two halves, one less colored than the other. When the F_2 is represented by a few individuals, the respective square contains a few dots or stripes.

At the right margin of Plates I and II one parental fore- and/or hind-wing of the species involved in the cross mating is given. These figures show the morphological distinction between the species crossed. For the cross *Colias crocea* x *C. hyale* a hybrid male is also presented. For the crosses *Pieris bryoniae* x *P. ergane* and *Leptidea morsei* x *L. sinapsis* enzyme data are not available, while three of the *Colias* have not yet been crossed.

Sterility Grades

By comparing the enumerated properties of hybrids, it is possible to arrange the hybrids in a series of decreasing fertility (or increasing sterility). Exact grading is not possible because the differences between several crosses were minimal or undetectable. In Table 1, left column, the presence of completely developed adult males and females in F_1, F_2 and R_1 is indicated by a cross, +. any departure from normal development is indicated by a reduced length of the respective arms of the cross: the left arm = size, the upper arm = number of offspring, right arm = development (crippling) and the lower arm = inviability. Lower numbers of one sex are identical with skewed sex ratio, a variable therefore not separately identified. Inviability is in part involved in the first three characters, while in the fourth arm the viability of the adults is to be understood.

Indices of hybrid sterility in Table 1 were derived by multiplying relative arm lengths with a full arm receiving a value of one, a case of complete fertility of both sexes for the three test generations would be 4 (full arms) x 2 (sexes) x 3 (generations) = 24. Total sterility would be 0. The values obtained are given in detail in Table 2.

Comparison of Crosses and Enzymatic Data

Enzyme dissimilarity (EDf), 1-$\bar{I}$, values are employed in the following rather than the enzyme identity ($\bar{I}$) values used by Geiger (1981) in the construction of dendrograms illustrating taxonomic affinities in the

Table 1.   Comparison of hybrid fertility (HF, left), hybrid sterility (HS) and enzymatic dissimilarity (EDf) values (right) (Geiger, 1982) in 13 taxa of European Pieridae. Degrees of hybrid sterility are based on properties of reporduction in the F_1, F_2 and R_1 generations.

Hybrid Fertility (HF)		Pairs of Species Crossed		Enzymatic Dissimilarity $1 - \bar{I}$ (dotted) / Hybrid Sterility (striped)
F_1 F_2 R_1				,3 ,4 ,5 ,6 ,7 ,8 ,9 1,0
♂ ♀ ♂ ♀ ♂ ♀				
+ + + + + +		Euchloe crameri – simplonia	4	
+ + + ⌐ + +		Pieris napi – bryoniae	76	
+ + + +		Colias australis – hyale	4	
+ + (⊤ ⊤)		Pieris rapae – mannii	25	
+ ⊢		Anthocharis euphenoides ♀ – cardamines	1	
+ ⊤		Colias crocea ♀ – hyale	1	
+ ⊢		Pieris mannii ♀ – napi	2	
+ ⊤		Pieris rapae ♀ – napi	2	
+ ⊤		Pontia daplidice ♀ – protodice	1	
⊣ •		Anthocharis cardamines Euchloe simplonia	4	
•		Pontia daplidice ♀ Pieris rapae	2	
				24 20 15 10 5 0

Key to symbols:

+   normal

⊢   undersized

⊤   lower numbers

⊣   crippled

⊥   inviabilized

•   no larval hatch

The relative length of an arm corresponds to the degree of effect.

Table 2.   The degree of hybrid fertility of both sexes in F_1, F_2 and R_1 generations and the total hybrid fertility (HF) versus hybrid sterility (HS) in the interspecific crosses in Pieridae.

Taxa Crossed		F_1		F_2		R_1			(HF)	(HS)
Female	Male	♂	♀	♂	♀	♂	♀		♂+♀	♂+♀
1. E. crameri x E. simplonia		4.00	3.00	3.75	3.75	3.90	3.75	=	22.15	1.85
2. P. napi x P. bryoniae		4.00	2.25	2.25	1.75	3.75	3.50	=	17.60	6.40
3. C. hyale x C. australis		4.00	4.00	—	—	3.50	3.30	=	14.80	9.20
4. P. rapae x P. mannii		4.00	3.25	—	—	(2.25)	(2.75)	=	12.25 (7.57)	11.75* (16.43)
5. A. euphenoides x A. cardamines		4.00	2.75	—	—	—	?	=	7.75	16.25
6. C. crocea x C. hyale		3.80	1.95	—	—	—	—	=	5.75	16.25
7. P. rapae x P. napi		3.00	2.75	—	—	—	—	=	5.75	18.25
8. P. mannii x P. napi		3.50	2.05	—	—	—	—	=	5.55	18.45
9. P. protodice x P. daplidice		3.00	1.10	—	—	—	—	=	4.10	19.90
10. E. simplonia x A. cardamines		1.60	0.05	—	—	—	—	=	1.65	22.35
11. P. daplidice x P. rapae		0.04	—	—	—	—	—	=	0.04	23.96

*Although in *rapae* x *mannii* the number of backcross matings achieved and eggs laid is 3.5 times greater than in *Euchloe* and *Colias* crosses, the number of adult offspring is 6.6 times smaller. Therefore, the sterility grade of R_1 (*rapae* x *mannii*) must be reduced from 5.00 (= 2.25 + 2.75) to 5.00 : (3.5 x 6.6) = 0.22.

Pieridae. It seemed appropriate to present his data as EDf values for comparison. The corresponding way to present the hybridization data was to use the hybrid sterility (HS) scale. In Table 1 (right hand column) the 0.3 - 1.0 portion of the EDf scale was arbitrarily juxtaposed to the whole (0 - 24) HS scale, because enzymatic I values below 0.3 were the lowest limit of enzymatic similarity that Geiger found.

Results

The comparative quantitative data are given in Table 2. The striking feature here is the high hybrid sterility (HS) values of crosses 4 - 11, which are related to the failure of F_2 and R_1. HS values are less in crosses 1 - 3. The extreme HS values found in crosses 10 and 11 reflect the fact that these resulted from mating individuals belonging to species of different genera. Although the crosses were arranged according to the rising HS values, the enzymatic dissimilarity (EDf) of the hybrids increases more uniformly than the HS values. However, considerable discrepancies exist between the HS and EDf values in crosses 1 - 4, all of which are taxa belonging to the lowest taxonomic level. In cross 1, HS is less than EDf, while in cross 3 HS is .3 greater than EDf, while in cross 2 HS is 31 times greater than EDf. Another discrepancy is found in cross 4 in which HS is more than 3 times larger than EDf.

The discrepancies between the HS and EDf values deserve further analysis. The pair *Pieris rapae* x *P. mannii* (cross 4) will be considered first. The two species here represent a case of full biological speciation in spite of such similarity of external appearances that the two species leads sometime to their false identification.

Pieris rapae - P. mannii. These two species are reproductively completely isolated, having an index of sexual isolation approaching unity in full sympatry, although not always syntopically (unpublished data). In spite of generalized morphological similarity, these species differ in at least 24 morphological characters found at all developmental stages, from egg to adult. In 19 crosses, normally developed individuals of both sexes occurred only when the mother was *rapae*, while with *mannii* mothers the females were missing with few exceptions (8%). The F_2 is completely blocked in both directions because the females in F_1 contain undeveloped eggs, usually producing no eggs at all (Figs. 1 and 2). Although the chromosome numbers are the same in both species ($N = 25$), chromosome pairing during meiosis of the spermatocytes (Fig. 3) is so highly disturbed that the fecundity of the males is 7 to 1000. From 32 back-crosses with females of both species in 6 of the 8 possible mating combinations 1,310 eggs were laid, but not more than 9 larvae hatched and 8 males and 1 female eclosed (0.68%). Three males were slightly crippled. No eggs were produced either from two F_1 x F_1 matings or from one R_2 backcross. It is
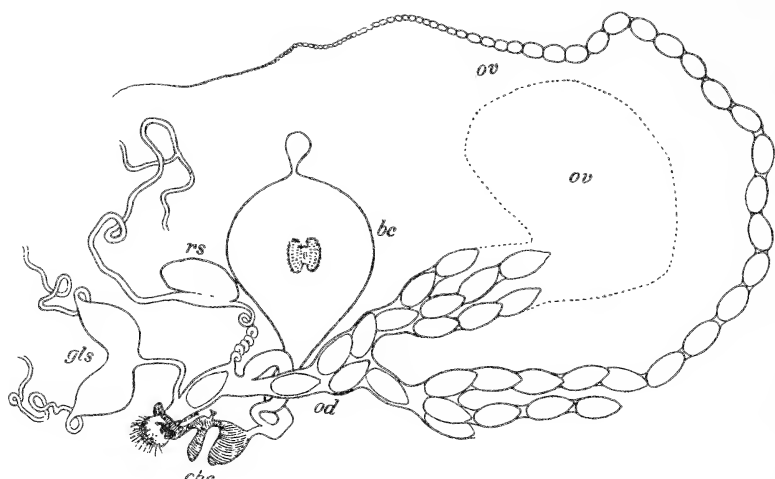
Fig. 1.　Internal and external female genitalia of *Pieris rapae* L. with normally developed ovaries of which only one ovariole is spread. (after Lorkovic', 1928).
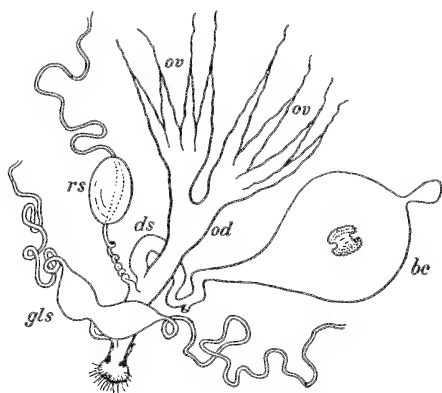
Fig. 2.　Female genitalia of an adult *Pieris rapae* x *P. mannii* hybrid with short ovarioles lacking eggs entirely. Note the other fully developed genital organs (the external genitalia removed). (after Lorkovic', 1928).
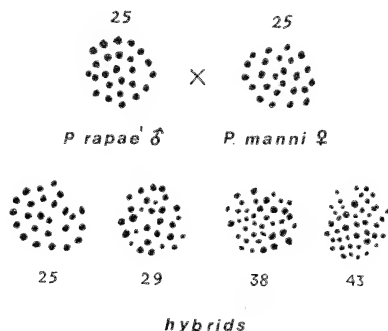
Fig. 3.　Metaphase chromosome plates of the first meiotic division in spermatogenesis of *Pieris rapae* x *P. mannii* with 25 bivalent chromosome (upper row) and their F_1 hybrids with different chromosome pairing, from normal 25 to 43, with only 6 chromosome pairing. Slides No. 0143, and 0139 (1934).

evident from these data that *P. rapae* and *P. mannii* are two reproductively incompatible taxa and that they cannot be regarded as anything but two full species, bearing all typical species properties. Nevertheless, the EDf value for these two species is 0.10, much less than the minimum of 0.20 - 0.30 suggested for such cases by Bullini, et.al. (1981) and nearly half that of the next two taxa.

Euchloe crameri - E. simplonia. These two species are clearly less genetically differentiated than the above *Pieris* species, yet their EDF value is 0.17, much larger than the value 0.10 for the two *Pieris*. It is worth recalling that until recently these two taxa were considered subspecies of *E. ausonia*, because of their morphological similarity and with separate distribution ranges. In fact, the nomenclature problem of this complex is far from satisfactorily resolved (Back, 1979). Since the results of many crosses are not yet available (Lorković and Back, in prep.), only corsses of *E. crameri* and *E. ausonia graeca* from Dalmatia and the Balkans will be considered here. *E. ausonia graeca* is very close to *E. simplonia*. There are neither mating barriers between them, nor any notably diminished hybrid fertility except in one feature (see below).

There is a well expressed, although incompletely explored, premating barrier between *E. crameri* and *E. a. graeca*. However, no disturbances of fertilization or of hybrid development have been noticed insofar as can be distinguished from breeding problems. It should be noted here that species of the genus *Euchloe* (and *Anthocharis*) are not convenient for crosses in which many individuals are needed, because the larvae are cannabalistic feeding on both nearby eggs and later other young larvae living on the same stem. Larvae are particularly vulnerable in the moulting stage. Thus usually not more than 20 pupae result from 100 - 150 layed eggs even with the best of care. When prolonged pupal diapause is added to these problems (diapause can be lasting 2, 3 or even 6 years) the possibility of distinguishing between breeding failure and hybrid sterility, i.e. the known inability of hybrid female pupae to terminate the diapause, is further reduced. Such prolonged diapause was found more frequently when *crameri* was crossed with *simplonia* than with *graeca*. In one large *simplonia* x *graeca* brood all F_1 females eclosed without prolongation, a sign of their close genetic affinities.

Only one true hybrid character appeared in *crameri* x *a. graeca* crosses: a form of protogyny caused by the absence of the diapause in the female F_1 pupae, while all male hybrid pupae overwintered. This case resulted in desynchronization of the sexes, although in nature such females could mate with males of the second generation of *crameri* where it is bivoltine. In the R_1 of *crameri* x *graeca* females with *graeca* males bivoltinism was absent, but appeared in less than half of the females in the reciprocal backcross of hybrid males with *graeca* females. Such cases of female bivoltinism is not rare in butterflies (Federley, 1953) and was found also

in a *Iphiclides podalirius* female x *I. (p.) feisthameli* male cross, two taxa with a narrow overlap zone in the eastern Pyrenees and with highly fertile hybrids.

The chromosome number N = 31 is the same in *E. crameri, E. simplonia* and *E. ausonia graeca* as is the case in all other Anthocarini so far determined.

As in all previous *Euchloe* hybidizations, a highly, though possibly not fully, fertile F_2 generation was produced, as is usual in hybridizations below the specific level. Thus *E. crameri* and *E. ausonia graeca*, and probably also *E. simplonia*, seem to have barely reached semispecific status and to lag in their genetic differentiation far behind the pair *Pieris rapae - P. mannii*. Nevertheless, the EDf value of the *Euchloe* hybrids was nearly twice as large as that of the *Pieris* hybrids, but neither their extent nor direction is consistent with the degree of genetic reproductive incompatibility.

Pieris napi - P. bryoniae. The findings of an EDf value as low as 0.008 for *napi - bryoniae* startled taxonomists acquainted with the matter (Courtney, 1982) because it suggested that *bryoniae* is a taxon ranking below that of a subspecies. It is less than probable that this result represents the true biological distance between the two taxa. The reasons are as follows: 1)the karyotype of *napi* is a constant N=25 throughout Europe, from Moscow to the Balkans and Pyrenees and the British Isles. In *P. bryoniae,* on the other hand, N is usually 26 - 27, sometimes 25 (SE Alps) or 28, with additional 0 - 3 supernumeraries (Lorković, 1968), 2) the F_1 males of *napi* x *bryoniae* hybrids are highly, and the F_1 x F_1 matings rarely, fertile due to the mostly infertile females.

The greatest obstacle to the successful reproduction of the hybrids in nature is the disruption of diapause in the hibernating female pupae (Bowden, 1953, 1955, 1957; Petersen, 1955, 1963). In spite of their normal development, non diapausing pupae produce highly infertile females. Combined with the univoltinism of the highland *bryoniae*, this excludes the hybrid females from the reproductive process and further reduces their already low fertility. Only backcrosses of the hybrid males with parental females can thus be successful. Due to bivoltinism of the mainly lowland *napi*, the occurrence of these backcrosses is low in nature. However, the sexual isolation is not complete, and there is a complicated interaction between lowland *napi* with the rather pure highland *bryoniae* populations in overlapping areas (Petersen, l.c.). On the one hand, there are examples of intrusion of the dominant *bryoniae* gene, *Br*, into lowland populations of *napi* (Lorković, 1969; Eitschberger, 1983). On the other hand, a study of the genetic composition of the *bryoniae-napi* populations from the upper Sava valley at the extreme southeastern outskirts of the Alps suggested that the *bryoniae* form there is not hybrid, as maintained earlier, but a reproductively isolated (from *napi*) form of *bryoniae*

karyotypically identical with the Alpine form (Lorković, 1968). For further genetic information about these taxa the cited work of Bowden and Petersen should be consulted.

More recently Geiger (1984) extended his studies of enzyme similarities to other European subspecies: *thomsoni* from the British Isles, *meridionalis* Heyne & Rühl, 1895 from Italy, *adalwinda* Fruhstorfer, 1909 from Scandinavia and *P. pseudorapae balcana* from Yugoslav Macedonia. The results were similar to those of *bryoniae*. The lack of difference between *adalwinda* and *bryoniae* is not surprising since they are nearly identical. Less persuasive is the close enzytmatic similarity of *balcana* and *napi*, which are essentially reproductively isolated. The karyotype of *balcana* is like that of *bryoniae*, containing 26 - 27 bivalent and 0 - 3 tiny univalent chromosomes, and different from the *napi* karyotype. *P. pseudorapae* Verity, 1911, from Anatolia and ssp. *suffusa* from the Transcaucasus (Lorković, 1968/69) are somewhat similar to the karyotype of *napi*. The taxa predominantly contain the 25 chromosomes characteristic of *P. napi*, while the *bryoniae* karyotype is less freqently represented. The *napi* karyotype, however, is seldom found in *balcana*.

In strong contrast according to the recent enzymatic data of Geiger (1984), the North-American *napi* group taxa are sufficiently different from *napi* and from each other to be considered species. This is in agreement with Eitschberger (1983) who listed *P. venosa, P. marginalis, P. virginiensis* and *P. oleracea* as distinct species. Although definitive publication on enzymatic similarity in these taxa is not yet available, the sexual isolation of North American *P. oleracea* and European *P. napi* is very incomplete. Since F_2 and F_3 generations of the respective crosses are obtained without difficulty, the genetic-reproductive isolation seems to be even less complete (see Bowden, 1972).

As an example, a cross deisgned to explain the lack of the dark upperside wing pattern of *P. oleracea* should be mentioned. *P. oleracea* was crossed with *f. "funebris"* (Lorković, 1971) which has a heavily pigmented phenotype, recessive with respect to wild type *napi*. In the F_1 the *napi* phenotype appeared. This shows that *oleracea* contains the dominant *napi* gene for the usual *napi* melanistic pigmentation. In spite of dominance, this gene is not expressed in the phenotype of *oleracea* suggesting a recessive suppressor gene is involved. Indeed, in the F_2 all combinations of characters of *napi, "funebris"* and *oleracea* were obtained. In one of the F_3 a pure stock of homozygous *"funebris"* appeared having the wing pattern only in traces, and thus analogous in appearance to *P. oleracea*. Obviously, the recessive gene for *"funebris"* pigmentation was combined here with a recessive homozygous supressor gene. Such an extensive genetic analysis would not have been possible if *oleracea* were genetically incompatible with *P. napi*, as suggested by Eitschberger (1983) and Geiger (1984). The taxon *oleracea* is genetically more closely

related to *P. napi* than *P. bryoniae* is related to *napi*, while enzymatically *oleracea* is more distant from *napi* than from *bryoniae*—another example of sterility versus enzymatic discrepancy.

The closeness of the *oleracea-napi* relationship is reflected also in the karyotype, both taxa having the same number of chromosomes (N = 25). Thus pairing of chromosomes in meiosis is not affected.

Least but not last, three of the five North American taxa are allopatric or only slightly parapatric with narrow zones of overlap, as illustrated by the extensive material analyzed and systematized by Eitschberger (1983). Accordingly, these taxa should be classified between subspecies and species not only genetically, but also on the basis of geographic distribution.

Crosses between Forms and Subspecies

That the low fertility and viability of the interspecific hybrids, found in these investigations, do not reflect adverse breeding conditions is evidenced by breeding variants of one and the same population as well as from crosses of taxa considered to be geographically separated subspecies.

1) As an example of the first kind, during the selection of the form *"confluens"* of *Pieris rapae*, inbreeding was carried out for 10 generations. The number of offspring gradually decreased due to diminution of pairing drive in males. After the tenth generation, a male was introduced from outside. Following this inbreeding was continued for 10 more generations. Consequently, the decrease of fertility was nothing other than inbreeding depression, documented so clearly by Oliver (1981). No true genetic incompatibility or sterility has been observed.

2) For crosses at the level of morphs or forms, breeding of *P. napi napi* (Zagreb) x *P. napi* f. *"sulphurea"* (England) should be mentioned. Neither mating behavior reluctance nor infertility occurred, so that homozygous double recessive *"sulphurea funebris"* could be obtained. A F_3 generation was, of course, necessary to get sufficient numbers of progeny.

3) Among the spatially separated subspecies, *P. napi* from Zagreb was crossed with ssp. *migueli* (Eitschberger, 1983) and with the ssp. *santateresae* (Eitschberger, 1983 = *dubia* Röber, 1908). Eitschberger provided specimens of these from Spain in 1972. It was found that *P. napi santatersae* mates normally with *P. napi napi*, yielding an abundant F_1 and F_2 without of occurrence of any diapause disturbances, confirming the subspecific nature of the taxon (Eitschberger, 1983).

However, with ssp. *migueli* from Picos de Europa *napi* males do not react promptly to *migueli* females, as 10-15 s were required for *migueli* females to quiet down following introduction of the *napi* males, although

the same delay was observed also when *migueli* males and females re-acted to one another. I had the impression that my laboratory was too warm and dry for ssp. *migueli* to thrive, which is in agreement with the fact that Eitschberger had better breeding success in Germany. Con-versely, I had more success than Eitschberger in breeding ssp. *santa-teresae* from Central Spain. Pairing of both Spanish subspecies progressed without disturbance and normally developed males and females, including diapause, were produced from 5 matings.

Crosses between several other subspecies involving fewer individuals progressed normally. Thus there is no reason to suspect faulty breeding conditions as the cause of sterility found in the other Pieridae crosses reported.

Chromosome Pairing and Sterility

Hybrid sterility is usually accompanied, if not a function of, deviations of chromosome numbers of the taxa crossed. Sterility is here reflected by the failure of the homologous chromosomes to pair during the maturation process of meiosis and is easily visible in equatorial plates of meiotic divisions of the spermatocytes in the hybrid testes. One example is illus-trated in Figure 3, for a *Pieris rapae* x *P. mannii* hybrid. Here, instead of 25 regularly paired chromosomes (bivalents), different numbers (25 - 34) of unpaired, univalent, smaller chromosomes can be detected. A recapitulation of data on chromosomal irregularities which are related to hybrid sterility is given in Table 3. The number of the testes and metaphase plates examined, the number of parental bivalent chromo-somes found as well as bivalents of the taxa crossed, their average num-ber, and the frequency of deviations in pairing are given.

Counting chromosomes in the testes of hybrids can be rather laborious due both to the scarcity of meiotic divisions and even more so due to the uneven chromosome plates in which some chromosomes cover and mask others using the paraffin microtome section method. In Table 3 only un-equivocal chromosome numbers are given, with the exception of the single *Anthocharis eupheoides* x *A. cardamines* cross of which only a single, much inclined plate of 35 ± 3 chromosomes could be approx-imately estimated.

The number of chromosomes is less variable within the testes of the same individual than between different individuals of the same cross. So in 19 examined crosses of *P. rapae* females and *P. mannii* males a single plate with 43 chromosomes was found while in the reciprocal cross with *mannii* females the much lower number 25 - 34 was common. The greatest chromosomal deviation from the norm in the present hybrid series resulted from a barely fertile backcross of *P. rapae* female x (*P. mannii* female x *P. rapae* male) male. The single male examined had 40

Table 3. Chromosome number (CN) in the metaphase plate of meiotic divisions of spermatocytes of parental and F_1 testes in the hybridization of closely related Pierid taxa. In taxa with unequal parental CN the mean value is set in parentheses. The difference between P and F_1 CN indicates failures in the pairing of homologous chromosomes and is expressed as frequency.

Taxa Crossed	Number		Chromosome Number				Frequency of Pairing Failure
	Testes Examined	Plates Observed	P	F_1 Mean	F_1 Range		
1. *Pieris rapae* ♀ x (*mannii* ♀ x *rapae* ♂) ♂	1	5	25	43	40-46		.42
2. *P. rapae* ♀ x *P. napi* ♂	2	1	25	40	40		.38
3. *P. mannii* ♀ x *P. napi* ♂	6	2	25	37.5	36-39		.33
4. *P. rapae* x *P. mannii*	13	10	25	38.4	25-43		.35
5. *Anthocharis cardamines* ♀ x *Euchloe ausonia graeca* ♂	1	4	31	47.7	44-49		.35
6. *E. ausonia graeca* ♀ x *A. cardamines* ♂	1	1	31	47	47		.34
7. *A. euphenoides* ♀ x *A. cardamines* ♂	1	1	31	38	38		.18

8. *P. ergane* ♀ x *P. napi* ♂	4	16	25.3 25	27.8	25-28	.09
9. *P. napi* x *P. (napi) bryoniae*	43	60	25 25-32 (27.6)	26.5	25-28	.05
10. *P. napi* x *P. (pseudorapae) balcana*	9	9	25 25-28 (27.1)	26.1	25-28	.04
11. *P. (napi) bryoniae* x *P. (pseudorapae) balcana*	9	19	(27.6) 25-28 (27.1)	26.3	25-28	.04
12. *P. napi santateresae* ♀ x *P. napi napi* ♂	5	14	25	25.2	25-25.5	.01
13. *P. napi migueli* ♀ x *P. napi napi* ♂	5	8	25.1 25	25	25	.004

As supernumeraries are about one quarter to a half the size of other chromosomes, they were calculated as 0.25-0.50 for one chormosome and added to the whole set in proportion to their frequency. Matings without sexual signs involved reciprocal crosses.

chromosomes in one and 46 in four metaphase plates, the extreme case in which only 4 chromosomes pair instead of 25, unexpected for backcross individual, which are mostly fertile.

Although the *Anthocharis* x *Euchloe* hybrids are at the bottom of the fertility scale (Tables 1 and 2), failure of their chromosomes to pair (34 - 35) is proportionally not greater than in the *Pieris* crosses (34 - 38) which are higher in respect to fertility. This circumstance may be due to the fact that the Anthocharini have 20% more chromosomes than Pierini. They therefore probably have about 20% shorter chromosomes on the average which diminish the probability for conjugation irregularities for about the same percent. That the sterility of *Anthocharis* x *Euchloe* crosses is even greater than would be indicated by the pairing disturbances above is evidenced by the frequent total degeneration of the testes, which can be reduced to a somatic testes envelope without any trace of germinal cells. Depending upon the variable number of paired chromosomes, the final process of spermiogenesis is interrupted at different maturation levels. Sometimes testes do not contain either any sperm bundle or initial germ cells. Nevertheless, in a large fraction of adult hybrid specimens the testes contain large numbers of sperm bundles, but these sperm are no more fertile than those from testes with only a few sperm bundles.

The *Pieris napi-bryoniae-balcana* group is as yet unresolved taxonomically. Karyological definition is also not precisely defined. Not only does the different specific chromosome number between *napi* and the other taxa make the degree of pairing failures uncertain, but further problems are encountered due to the inconstant chromosome number in *bryoniae* (and *balcana*) itself, varying from N = 25 - 28. In *bryoniae* even higher numbers, 29, 30, 31 and 32, have been recorded from four individuals (Lorković, 1968). As a further complication, 1 to 3 minute univalent supernumerary chromosomes occur in a various percentage of *bryoniae* individuals. These usually lie off the equatorial plate and pass, mostly undivided, into only one daughter cell, presumably without a deleterious genetic effect (White, 1973). The supernumaries thus were neglected in the present calculations.

Eighty-nine *bryoniae* specimens from nature and 74 hybrids of F_1, F_2 and R_1 - R_4 have been karyologically examined (Lorković, 1968). In the F_1 hybrids, N = 25 and 26 were predominant (13 and 10 individuals respectively). The other numbers occurred in a small number of individuals, and 33 - 44 chromosomes were counted in a backcross individual. The known variation of hybrid fertility or sterility of *napi* x *bryoniae* crosses can be at least partly attributed to this inconstant number of *bryoniae* chromosome, thus producing the observed pairing failure of 0.05 (Table 3). However, in *napi-bryoniae* no remarkable irregularities in chromosome pairing can be cited in concordance with the finding of rather high male fertility in *napi* x *bryoniae* hybrids, but not in females which are

highly sterile. The effect is probably due to genetic factors and not chromosome mechanics.

One of the proportionally lowest values of chromosome pairing failure in crosses between two clearly defined species is the case of *Pieris ergane* x *P. napi*. This case is included although the enzyme relations are not yet known. The sterility of the hybrids of these two species is so low that even a partially fecund F_2 can be produced, while the backcrosses are normally fertile. This high fertility coincides with low failure rate of chromosome pairing, .09, falling in value between the full specific and subspecific stage. Nevertheless, *P. ergane* and *P. napi* are fully sympatric, and, although very close, both karyologically and morphologically, no worker has regarded these as other than good species.

The lowest number of irregularities of meiotic chromosome pairing occur in crosses of *Pieris napi* subspecies in which 25 pairs of chromosomes are regularly found. The cross *P. napi santateresae* x *P. napi napi* yielded a tiny supernumerary which disappeared in 5 back-crosses with ssp. *migueli*.

Unfortunately, the only fixed and prepared testes of *Euchloe simplonia* x *E. ausonia graeca* proved to be too old and without meiotic divisions. Its normal size and complement of ripe sperm is in agreement with the high fertility of F_1 individuals. It is reasonable that the meiotic divisions are normal.

Although a substantial number of karyotypes reported are not known from more than one equatorial plate, the data in general are in accordance with a decreasing trend of hybrid sterility as shown in Tables 1 and 2.

Discussion

Comparison of electrophoretic enzymatic dissimilarity and hybrid sterility in the Pieridae shows that differences between the results of both procedures are relatively much smaller between species which belong to two genera, subgenera or groups of species than among taxa at the lowest taxonomic rank, such as subspecies, semispecies or sibling species. The question here is to explain this discrepancy and to decide which of the methods is more reliable for the estimation phylogenetic relationships. If enzyme similarity is the measure of relationships, how is it possible that two entities biologically as well differentiated as *P. napi* and *bryoniae* are enzymatically almost identical; while *E. crameri* and *E. simplonia*, which are more compatible genetically, show a disproportionally high enzyme diversity, 21 times higher than in *bryoniae-napi* and nearly twice as high as the reproductively highly incompatible *rapae-mannii* pair?

One reason for the discrepancy may be that the taxonomic estimation of divergence at low levels is not sufficiently confined, i.e. the taxonomy at

the lowest levels is not precisely enough graduated to produce unequivo-
cal categories. One approach to correct this weakness in taxonomy would
be broadening the biological species concept to cover partially hybridiz-
ing taxa, combined with a stronger emphasis on spatial and ecological dif-
ferentiation. More than twenty years ago Ehrlich (1961) emphasized that
the biological species concept was outliving its usefulness. Nevertheless,
in 1982 Ehrlich and Murphy explained "that sympatric synchronic pop-
ulations that do not interbreed should be considered to belong to separate
species" or "if it were certain that successful interbreeding is not possible.
. .would we elevate. . .to specific status".* Obviously the gap between the
biological species concept and the nonbiological is not so serious as seems
at first glance, and that it is not necessary to create more confusion where
enough is already present. Although the incompleted stage of speciation
does not have a generally accepted taxonomic term (semi species or
similar), such a category is indispensable in evolutionary biology as well
as in taxonomy itself. Clearly it is incomplete speciation that is the heart
of the nearly hundred years of argument over the *napi-bryoniae* problem.
This situation contrasts with that of the remarkable specific stability in
the genus *Leptidea*, of which *L. morsei* cannot be distinguished over its
entire palearctic range from Far East to eastern Europe, including its
invariable and usual karyotype of N = 54.

Discrepancy among taxonomist's views also arises from unequal and
unevenly developed isolating mechanisms found during the initial phases
of speciation. For example, *Euchloe crameri* appears sexually separated
from *E. simplonia*, but there are no other reproductive disturbances
characteristic of higher rank of speciation. On the other hand, these two
taxa behave like two subspecies in being almost completely allopatric.
Therefore, as usual in such situations, the question arises as to how much
the differentiation is due to an intrinsic genetic barrier and how much is
due to geographic and ecological displacement.

In evolutionary processes, isolating mechanisms frequently appear
independent from one another and at unequal rates. Hybrid incom-
patibility may arise between separate taxa, reflected in the infertility of
the female sex, before the aquisition of a premating barrier. Such a situa-
tion is found for *Pieris napi* (Europe) and *P. dulcinea psuedonapi*
(Japan) (unpublished), or in the reverse sequence, as already described
for the *Euchloe* pair.

A serious obstacle to the use of enzymatic differences in taxonomy is the
inequality of the EDf levels characteristic of species in different sys-
tematic groups. To mention only a few examples in Lepidoptera, Racheli,
et al. (1984) found average EDf values between 0.15 and 0.11 in four

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*The excellent paper of Murphy and Ehrlich (1984) appears too late to be incorporated in this
paper. I agree with several good points made by these authors concerning the future of taxo-
nomic work with the Lepidoptera.

among six south european geographic subspecies of *Parnassius apollo*, while the remaining two had 0.09 and 0.08. If the taxonomic levels of this group were to be estimated according to the criteria used for *Pieris rapae* and *P. mannii* (EDf = 0.10) then most of these subspecies would have to be classified as species. In the case of *P. apollo*, ssp. *hispanica*, perhaps also ssp. *pumilio*, such a conclusion would be valid if hybrid sterility were found experimentally, as enzyme criteria alone would be insufficient. The claim that at least one, if not all three, of the *P. apollo* subspecies should be considered species can be decided only by crossings. Then enzymes can be viewed as a stimulus for crossing experiments. In any case, it would be rewarding to perform hybridization experiments between some well differentiated subspecies to know finally how clearly they are reproductively differentiated.

Such uncertainties have been known for some time. Originally it was considered that greater EDf differences exist between taxa which are above the level of genus, but Bullini, et al (1981) emphasized that no rule exists and the distance between failies can be very large although in some cases not larger than between species.

On the other hand, enzyme differentiation does not appear to be a causative factor of reproductive separation, but rather an effect of isolation. Their evolutionary significance thus appears to be similar to that of other genes which influence small morphologic changes, as for example the specific genitalia which mostly do not impede hybridization. Thus the genitalia are much less efficient than premating olfactory obstacles. Natural copulation between *C. hyale* and *C. australis* is completely impossible, but mating ensues in reciprocal directions as soon as the olfactory barrier has been artificially removed (Lorković, 1953 and unpublished data). As with other characters, those enzymes selected for analysis may also well affect conclusions of relationships.

Speciation appears to be a capricious event and is not only a simple quantitative process, solely due to an accumulation of genetic differences. Speciation is clearly less dependent or independent of merely allelic alterations and substitutions. Ayala (1975), Oliver (1978), Bullini and Sbordoni (1980), discussing genetic differentiation and hybrid incompatibility, all point out that electrophoresis of enzymes cannot reveal more than 30% of all genetic differences, while other differences, such as those of regulatory genes are not accessible to this technique. Regulatory genes are responsible for the coordination of embryonic development, growth and differentiation, all of which are crucial for the success of specific hybridization. Chromosomal rearrangement may also have an important role here in agreement with the absence of regular chromosomal pairing in hybrids at the species level described in this paper.

Enzyme electrophoresis is without question of great significance to the

study of genetic differentiation of populations, but it would appear that the method is of most value at the micro evolutionary level and not as an infallible device for delimiting taxa since genetic reproductive isolation does not always coincide with any given amount of enzyme diversity. Since many extensive discussions of this problem have been made elsewhere, the results of the present contribution mainly serve to issue caution for the careful systematic interpretation of enzyme electrophoresis.

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Variations in the Wing Venation of *Pteroma plagiophleps* Hampson (Lepidoptera: Psychidae)

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Abstract. Studies on the wing venation of *P. plagiophleps* Hamp., (Psychidae) collected from different host plants and localities in Kerala State (India) have revealed the occurrence of 6 types of venational patterns in that species. Venation of moths within any given population sample also varies. Most of the observed variations related to the forewing veins 4 & 5, 8 & 9 and 11 & 12. Three of these venational patterns agreed with the venation described for the species, *P. plagiophleps, P. dealbata* Dierl and *P. postica* Sonan respectively. The study reveals the unreliability of using venation for the segregation of species belonging to the genus *Pteroma*. Further studies involving the morphology of adult as well as larval parts are required to resolve the correct identities of species belonging to this genus.

Introduction

The bagworm, *Pteroma plagiophelps* Hamp. is an important defoliator of several tree species in India. It was first described by Hampson (1892) from Sri Lanka (Ceylon). In southern India it was recorded as a pest of *Tamarindus indica* (Caesalpiniaceae) by Ayyar (1940). Aiyer (1944) and Das (1956) recorded it as a minor pest of *Punica granata* (Lythraceae) and *Camellia thea* (Theaceae) respectively. Recently Nair et al. (1981) reported heavy defoliation of *Albizia falcataria* (Mimosaceae), in forest plantations. It was recorded from different parts of the State, defoliating *Delonix regia* (Mimosaceae), planted as avenue trees (Mathew & Nair, 1983).

In spite of such great economic importance assigned to this species, its identity is still in confusion. Segregation of taxa to the generic level is based mainly on the wing neuration and characters of leg and antennal structure (Hampson, 1892). Dierl (1971) who revised the asiatic fauna used venation as an important character for segregation of various taxa. However, wing venation previously had been shown to be too variable to have much of a classificatory value (Davis, 1964). During a study of the bagworm, *P. plagiophleps* collected on different tree species in Kerala, I observed considerable variation in the venational pattern, which causes confusion in their taxonomic identities. Earlier workers (Aiyer, 1944;

Das, 1956) also have observed some anomalies in the venation of specimens. The present study was undertaken mainly to find out the extent of variations in this character and to determine the dependability of this character in determining the taxonomic position.

Materials and Methods

Insects used in this study were obtained from pupae collected at 5 localities in Kerala State in India as follows: Vazhachal, on *Albizia falcataria*; Puthukad, on *Delonix regia*; Trichur, on *Tamarindus indica*; Mannuthy, on *Emblica officianalis* (Euphorbiaceae) and Trivandrum, on *Syzygium cumini* (Myrtaceae). Wing venation of 10 moths selected at random out of a large sample collected from each of the above hosts were studied except for the last, for which only one moth was available.

Results and Discussion

The wing venation of *P. plagiophleps* as described by previous workers (Hampson, 1892; Dierl, 1971), is characterized by the possession of nine veins in the forewing and seven in the hindwing. In the forewing, veins 4 and 5 originate from the same point, 6 and 7 are absent, 8 and 9 are stalked and 11 and 12 are shortly anastomosing. In the hindwing, vein 6 is absent and the cell is open.

The venational patterns noticed in this study are listed in Table 1. The venational pattern varied among the individuals. Among 41 moths studied, only one collected from *A. falcataria*, showed conformity with the typical venation of *P. plagiophleps*. Most of the observed variations related to the forewing veins, 4 & 5, 8 & 9 and 11 & 12. Hindwing venation remained more or less constant. The venational patterns noticed in this study may be classed as follows:

A. Forewing with veins 11 and 12 anastomosing for a short distance.

B. Forewing with the veins 11 and 12 remaining free.

Under each of these categories, 3 sub-types were also present.

a) Forewing with veins 4 & 5 originating from the same point, and veins 8 & 9 remaining stalked (Fig. 1 c, f).

b) Forewing with veins 4 & 5 stalked and veins 8 & 9 originating from the same point, there being no stalking (Fig. 1 b, e).

c) Foreing with veins 4 & 5 and 8 & 9 borne on stalks of equal or variable lengths (Fig. 1 a, d).

Of the moths examined in this study, only 6 possessed shortly fused veins 11 & 12 in the forewing (category A). Of these only one conformed to the description of *P. plagiophleps* given by Hampson (category A, a - Fig. 1c). Others were either with stalks for veins 4 & 5 and 8 & 9 or with stalk only for the veins 4 & 5.
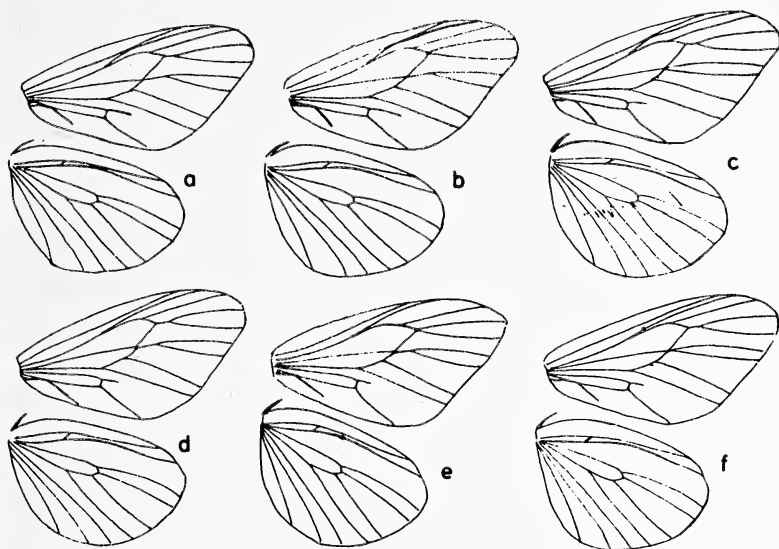
Fig. 1a-f.   Venational types in *Pteroma plagiophelps* Hampson.

Thirty five moths belong to the category B (i.e., with forewing veins 11 & 12 remaining free). Of these, 24 had stalks for veins 4 & 5 and 8 & 9. In 9 moths only the veins 4 & 5 were stalked and in the remaining the stalk was for the veins 8 & 9.

As mentioned earlier, anomalies in the wing venation of *P. plagiophleps* have been noticed by Aiyer (1944) and Das (1956). In moths studied by them the forewing veins 11 and 12 were free, veins 4 & 5 and 8 & 9 were stalked (category B, c; Fig. 1d). Dierl (1971) has described species of similar venation as *P. dealbata* from specimens collected in China. Similarly, the venational type wherein the forewing veins 11 & 12 are free with only the veins 4 & 5 remaining stalked (category B, b; Fig. 1e) have been recognized as *P. postica* by Sonan (1935) in Taiwan (Formosa). The occurrence of these species in the Indian subregion has not been reported. The inter- and intrapopulation variations observed in this study clearly indicates that venation cannot be considered as a stable character for delineation of taxa at least in the bagworm genus *Pteroma*. A detailed taxonomic revision involving studies on the morphology of adult as well as larval parts may be required to resolve the correct identities of species belonging to this genus.

J. Res. Lepid.

Table 1.   Venational characteristics of *Pteroma plagiophleps* collected on different hosts.

	Category A			**Category B**			
	Forewing veins 11 & 12 fused			Forewing with veins 11 & 12 free			
Host Species	4 & 5 free 8 & 9 stalked	4 & 5 stalked 8 & 9 free	4 & 5 and 8 & 9 stalked	4 & 5 free 8 & 9 stalked	4 & 5 stalked 8 & 9 free	4 & 5 and 8 & 9 stalked	Total No. of insects Examined
	(a)	(b)*	(c)*	(a)*	(b)	(c)	
Albizia falcataria (Loc. Vazhachal)	1	2	1		2	4	10
Delonix regia (Loc. Puthukad)					3	7	10
Emblica officianalis (Loc. Mannuthy)		1		1	2	6	10
Tamarindus indicus (Loc. Trichur)			1	1	2	6	10
Syzygium cumini (Loc. Trivandrum)						1	1
TOTAL	1 (2.34%)	3 (7.31%)	2 (4.87%)	2 (4.87%)	9 (21.95%)	24 (58.53	41

Category A. a — Venation of *P. plagiophleps* (Hampson, 1892; Dierl, 1971)
Category B. b — Venation of *P. postica* (Sonan, 1935)
Category B. c — Venation of *P. dealbata* (Dierl, 1971)
*New venational types recorded in this study.

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Diversity and Species Richness of Butterflies and Skippers in Central Spain Habitats

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Abstract. Local species number and diversity of butterflies from the more common habitat types in the Tagus Valley of central Spain are presented. Butterfly faunas are richest in less disturbed, better preserved shrublands with accompanying forest, particularly in "quejigares" forest dominated by the mediterranean oak *Quercus faginea*.

Introduction

The complexity of herbivorous insect communities generally reflects the diversity of the habitats or communities in which they occur (recently Strong & Levin, 1979; Templado, 1982; Lawton, 1983, among others). This observation has been considered in analyzing the butterfly and skipper faunas from major vegetational communities in the Tagus Valley of central Spain. The objective of this study is to compare butterfly diversity from a variety of habitats and to assess their relative conservation value since species number and diversity are the criteria most commonly used to assess wildlife conservation potential of habitats (Margules & Usher, 1981).

Material and Methods

The study area is 6000 sq. km located in the center of the Iberian Peninsula, between the Sistema Central Mountains and the Tagus River (Fig. 1).

This is a flat region. The substrate is mainly sedimentary; sands (Northwestern portion) and calcareous and chalky rocks (Southwestern, Southern and Eastern portions). All of the geological formations in this region are Miocene.

The Tagus Valley climax vegetation consists of evergreen *Quercus rotundifolia* and mediterranean oak (*Quercus faginea*) forests (Rivas Martinez, 1982). But well-preserved forests are rare. When these forests are altered, in the usual course of events, by human disturbance, a chaparral succeeds and *Quercus coccifera* shrubs dominate. When chaparral is also eliminated, an "esparto" grassland will occur (see Fig. 2). The dominant floral elements in these and the other major natural
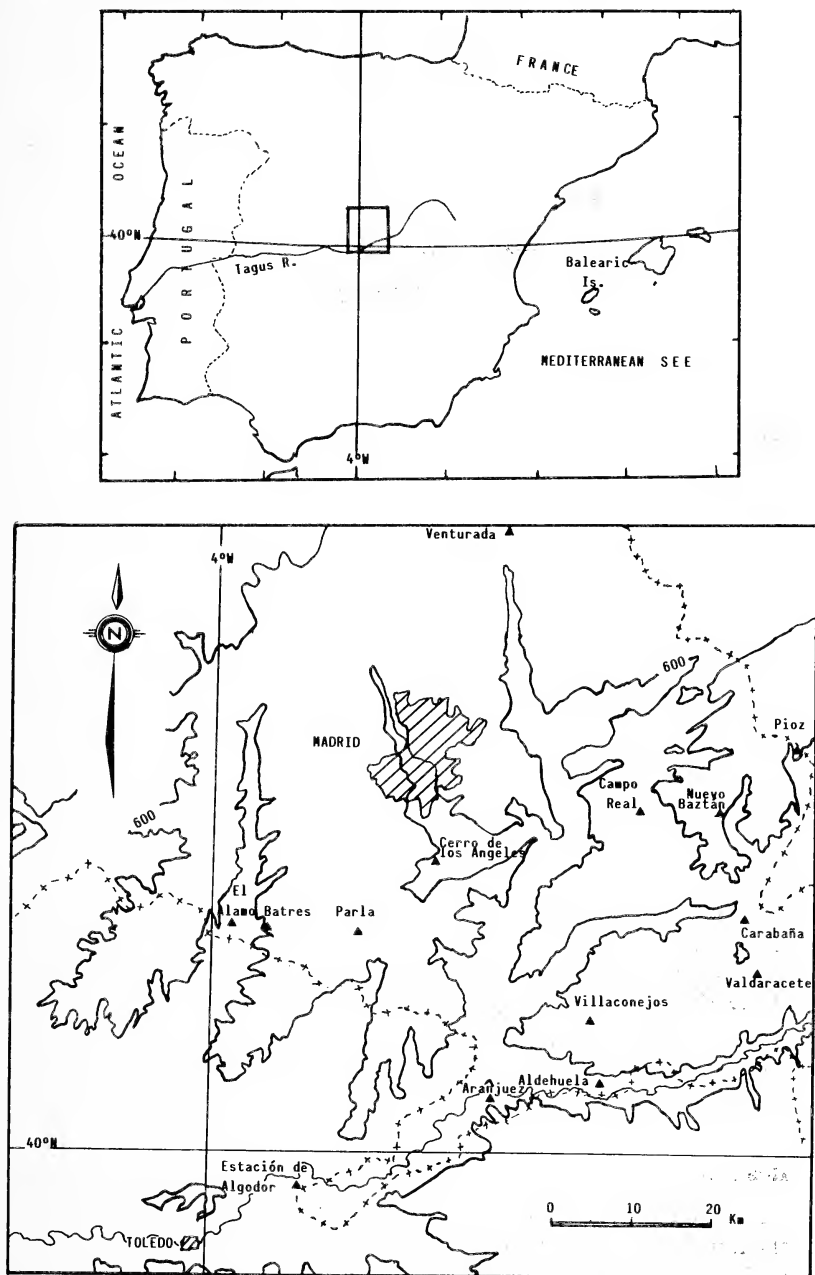
Fig. 1.   Maps showing the location of the area in Spain (above) and the localities
in the area (Tagus Valley, below).
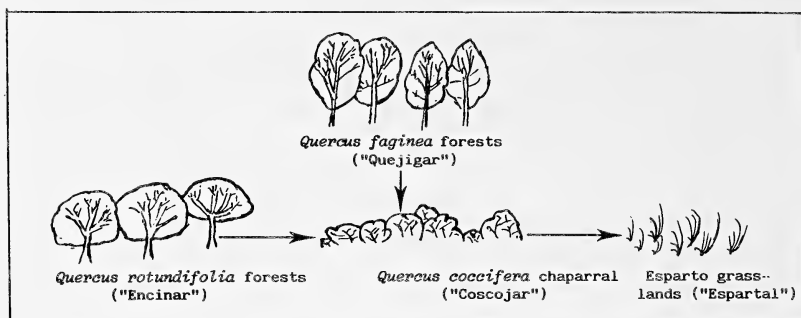
Fig. 2. Dynamism of the plant communities in the Tagus Valley.

habitats of the Tagus Valley are given in Table 1. In addition, ruderal communities, resulting from direct human impact such as those associated with farmlands, occur in the area. And, finally riparian communities exist limited to the immediate borders of river banks.

The general intensive degradation of the local vegetational communities resulting from agricultural and industrial activities have made woodlands rare while shrub steppes abound. Agricultural landscapes, mainly cereal fields, olive groves, orchards and vineyards predominate.

This study is based on a sample of nearly 6000 butterflies and skippers (Papilionoidea and Hesperioidea), captured during the period 1975-1983, in 79 localities throught the Tagus Valley (Viejo, 1983). At least four sampling localities with each of seven vegetational communities were sampled. As far as the work itself is concerned, we have established these seven vegetational communities to include: "Encinares" (*Quercus rotundifolia* forests), "quejigares" (*Quercus faginea* forests), "coscojares" (*Quercus coccifera* chaparral), "espartales" (esparto grasslands), "secanos" (dry croplands), "riberas" (riparian forests) and "regadíos" (irrigated croplands).

A diversity index at each sampling site has been done using Shannon-Weaver's coefficient (Margalef, 1957):

$$H = - \ p_i \ \log_2 p_i$$

Where H is Diversity; $p_i = N_i/N$; N_i = number of species i; and N = specimen numbers.

Results

Table 2 gives the Tagus Valley butterfly and skipper species list, with the number of species and the diversity of the two richest localities from each vegetational community. The highest number and diversity of species occurs on "quejigares" (Figs. 3 & 4). At one of these locations, Pioz, almost 30% of the Iberian species occur. The "quejigares" oak

Table 1.   Dominant floral elements in the major natural habitats of the Tagus Valley. C. D.: Conservation Degree, according to Van Maarel's classification (1975).

"ENCINARES" (Quercus rotundi-folia forests)	"COSCOJARES" (Quercus coccifera chaparral)	"QUEJIGARES" (Quercus faginea forests)	"ESPARTALES" Esparto grasslands	"RIBERAS" (Riparian forests)
Quercus rotundifolia	Quercus coccifera	Quercus faginea	Stipa tenacissima	Ulmus minor
Rhamnus alaternus	Rhamnus lycioides	Rosa micrantha	Asphodelus albus	Populus canescens
Ruscus aculeatus	Jasminum fruiticans	Crataegus monogyna	Rosmarinus officinalis	Populus nigra
Crataegus monogyna	Ephedra major	Arctostafyllos uva-ursi	Genista scorpius	Arum italicum
Genista scorpius	Rosmarinus officinalis	Lavandula latifolia	Arrhenatherum erianthum	Scirpus holoschoenus
Juniperus oxycedrus	Thymus vulgaris	Thymus vulgaris	Avena bromoides	Conium maculatum
Rubia peregrina	Genista scorpius	Genista scorpius	Dactylis hispanica	Brachypodium phoenicoidis
Lonicera etrusca	Asphodelus ramosus	Colutea arborescens	Bupleurum fruticescens	
Daphne gnidium	Bupleurum frutice-scens	Cephalanthera alba		
Cistus ladanifer	Colutea arborescens	Viola wilkommii		
C.D.: Semi-Natural	C.D.: Semi-Natural	C.D.: Natural	C.D.: Agricultural	C.D.: Agricultural

forests produce the highest diversities of all sampled localities in this region.

The selected "coscojares" (*Quercus coccifera* chaparral) also are comparatively rich, including the well-known localities at Aranjuez and Campo Real. The former is a "coscojar" (evergreen oak forest), and the second a mixed "coscojares-quejigo" forest (Fig. 2).

The evergreen oak forests show more moderate species richness, although less than the one might *a priori* predict, from the climatic nature in the Tagus Valley.

Noteworthy also is the greater richness of the dry croplands ("secano") in comparison to the "espartales", theoretical second replacement stage of the climatic forest (Fig. 2).

Riparian habitats also exhibit reduced richness than might be expected for a climax vegetational community.

Finally, note that the most impoverished localities are the irrigated croplands (regadío).

Discussion

Quejigo forests clearly present the richest butterfly and skipper faunas in the Tagus Valley. This is probably related to the superior conservation status, that is, less disturbed nature of these plant communities (Tem-
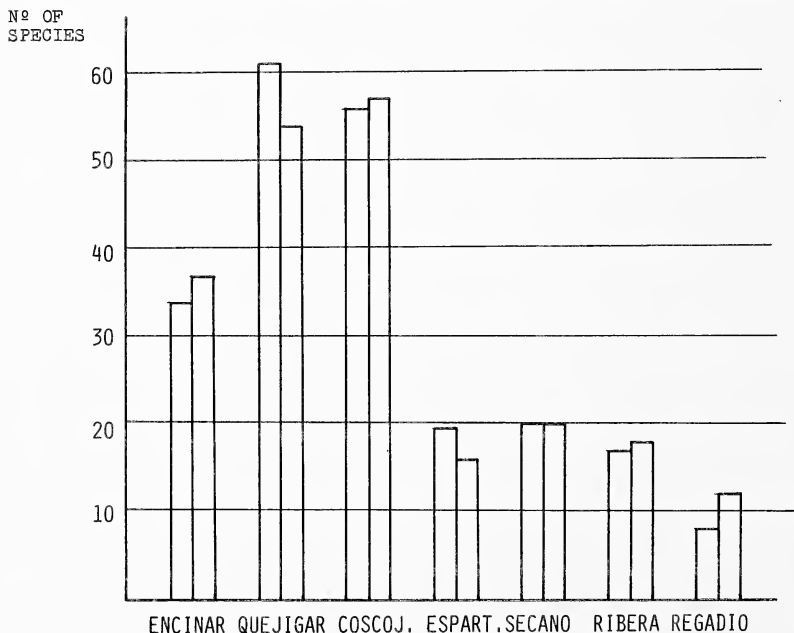
Fig. 3. Number of species of the two richest localities of each landscape.
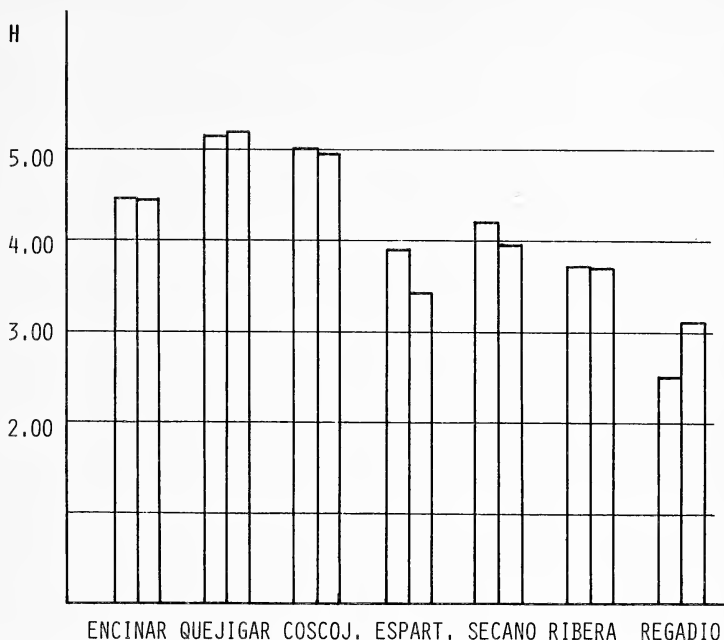
Fig. 4.   Diversity of species of the two richest localities of each landscape.

plado, 1982; Lawton, 1983). Thus these mediterranean oak forest should be considered the highest conservation priority in the Tagus Valley.

The "coscojares" also have a high faunal richness, close to that of the "quejigares". This may be attributed to the relative structural similarity of these shrublands with the climax woodlands, since they only vary by the elimination of the tree layer of evergreen oaks or "quejigos". This shortened evergreen oak forest richness, slightly less than that of the autoctonous woodland is the result of intensive habitat disturance where the shrub layer has been considerably altered and/or destoryed by man.

Dry croplands maintain a surprising faunal richness largely produced by the presence of marginal plant communities, particularly weeds typical to olive groves, vineyards, etc. This vegetation ("arvense") supports a substantial butterfly and skipper community.

River margins are extremely degradated in the Tagus Valley, especially the shrub component of the community, thus their faunas are impoverished.

Irrigated croplands are the very poorest habitats for butterflies and skippers. These areas are subject to the most drastic alteration through irrigation, the use of pesticides and herbicides, and other agricultural activities.

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Table 2.

Top section — species columns:

Aporia crataegi · Pieris brassicae · Pieris manni · Pieris napi · Pieris rapae · Pontia daplidice · Euchloe ausonia · Euchloe tagis · Anthocharis belia · Anthocharis cardamines · Zegris eupheme · Colias australis · Colias croceus · Gonepteryx cleopatra · Gonepteryx rhamni · Leptidea sinapis · Coenonympha dorus · Coenonympha pamphilus · Brintesia circe · Chazara briseis · Hipparchia semele · Hipparchia statilinus · Pseudotergumia fidia · Satyrus actaea · Melanargia ines · Melanargia lachesis · Melanargia occitanica · Maniola jurtina · Hyponephele lupinus · Pyronia bathseba · Pyronia cecilia · Pyronia tithonus · Pararge aegeria · Lasiommata megera · Limenitis reducta · Vanessa atalanta · Vanessa cardui · Inachis io · Polygonia c-album · Nymphalis polychloros · Euphydryas desfontainii · Melitaea deione · Melitaea didyma · Melitaea phoebe · Issoria lathonia

Bottom section — species columns:

Pandoriana pandora · Fabriciana niobe · Brenthis hecate · Libythea celtis · Callophrys rubi · Strymonidia spini · Nordmannia esculi · Quercusia quercus · Tomares ballus · Lycaena phlaeas · Heodes alciphron · Lampides boeticus · Syntarucus pirithous · Philotes abencerragus · Philotes panoptes · Glaucopsyche alexis · Glaucopsyche melanops · Iolana iolas · Celastrina argiolus · Zizeeria knysna · Cupido minimus · Cupido osiris · Plebejus pylaon · Polyommatus icarus · Agrodiaetus escheri · Agrodiaetus thersites · Lysandra albicans · Lysandra bellargus · Aricia cramera · Papilio machaon · Iphiclides podalirius · Zerynthia rumina · Carcharodus alceae · Carcharodus lavatherae · Carcharodus narrubii · Pyrgus onopordi · Pyrgus serratulae · Spialia sertorius · Syrichtus proto · Thymelicus acteon · Thymelicus lineola · Thymelicus sylvestris · Gegenes nostrodamus · Erynnis tages

Site	Number of Species	Diversity	Habitat Type
Nuevo Baztán	34	4.46	"Encinar"
Villaconejos	37	4.45	"Encinar"
Pioz	61	5.14	"Quejigar"
Venturada	54	5.18	"Quejigar"
Aranjuez	56	5.02	"Coscojar"
Campo Real	57	4.97	"Coscojar"
Carabaña	19	3.89	"Espartal"
Cerro de los Angeles	16	3.42	"Espartal"
Batres	20	4.19	"Secano"
Valdaracete	20	3.39	"Secano"
El Alamo	17	3.72	"Ribera"
Aldehuela	18	3.70	"Ribera"
Estación de Algodor	8	2.49	"Regadío"
Parla	12	3.11	"Regadío"

Artificial Raising of Lignicolous Lepidoptera[1]

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Abstract. Two alimentary media are described—one synthetic the other
semisynthetic—on which eight species of lignicolous Lepidoptera have been
raised to the imago stage.

Introduction

Bottger (1940) pioneered the development of artificial diets for raising Lepidoptera. He studied the chemical composition of the green plants associated with the survival, growth and metamorphosis of *Pyrausta nubilalis* Hubner (European corn borer) and in 1942 managed to produce an alimentary medium composed of casein, fats, salts, vitamins, agar and water.

Since then artificial diets have been successfully used with over 250 species of these insects, generally from the following families: Hepialidae, Aegeriidae, Gelechiidae, Oecophoridae, Yponomeutidae, Plutellidae, Tinaeidae, Lyonetiidae, Cossidae, Eucosmidae, Tortricidae, Galleriidae, Crambidae, Phycitidae, Pyralidae, Lasiocampidae, Attacidae, Bombycidae, Papilionidae, Pieridae, Nymphalidae, Hesperiidae, Geometridae, Sphingidae, Notodontidae, Lymantriidae, Noctuidae and Arctiidae (Notario, 1978a).

Material and Methods

Since 1973 research has been carried out in the Department of Zoology and Entomology (Escuela Técnica Superior de Ingenieros de Montes) into artificial raising techniques, the main objective being to obtain adult lignicolous Coleoptera. However, attempts have also been made to extend our field of study to those species of other orders whose feeding habits are similar. It should be kept in mind that one of the diets we based our initial work on (Gardiner, 1970) was a modification of that used by MacMorran (1965) to raise *Choristoneura fumiferana* Clemens a spruce and fir boring Lepidopteran.

This enabled us to raise *Aegeria apiformis* Clerck and *Paranthrene tabaniformis* Rottemburg, both lignicolous aegeriids attacking poplars (Notario, 1978b).

Encouraged by these results and thanks to grants made on the one hand by the Scientific and Technical Assessment Commission and on the other by an agreement between the Insect Pests and Phytopathological Inspection Service and the School of Forestry, we continued our work a number of different media being produced.

Two of these media were eventually found to satisfy the food requirements of the insects treated. The first is composed as follows:

Distilled water...25 cc
Agar ....3,5 g
Cellulose...2 g
Glucose ....1,5 g
Brewer's yeast...3 g
Vitamin free casein.....................................1,2 g
Saccharose ....2,5 g
Ascorbic Acid..0,4 g
Benzoic acid...0,1 g
Salt mixture ....1 g
Vitamin solution.......................................2 cc
Nipagin solution

The Nipagin solution consists of 1 g of methyl-p-hydroxybrenzoate in 5 cc of 70° alcohol. Both the salt mixture and the vitamin solution have been described elsewhere (Notario and Baragaño, 1978).

The composition of the second medium, semisynthetic this time, is as follows:

Distilled water...200 cc
Agar...10 g
Specific component ....44 g
Brewer's yeast...11 g
Nipagin solution
Benzoic acid ....1 g
Maize semola ....22 g
Wheat germ..44 g
Ascorbic acid ....0,6 g

"Specific component" is the denomination given to the immature insect's food in nature. This material is dried, blended and sterilized, at which point it is ready for mixing in the diet.

For both the synthetic and the semisynthetic media, the agar-water solution is heated on a hot plate until a gel is formed. Then the nipagin solution and benzoic acid are added and carefully mixed. The remaining components are now added with the exception of the ascorbic acid and vitamin solution in the first medium and the ascorbic acid in the second. The resulting mixture is allowed to cool to 60°C when the final components are added. It is now ready for distribution in the breeding chambers or for storage in hermetically sealed jars at 2-3°C.

Breeding chambers and the cages where they are housed have been described by Viedma *et al.* (in press).

Results

Eight species of Lepidoptera have been successfully raised from various larval stages to adulthood. They were as follows:

Family AEGERIIDAE
Synanthedon vespiformis Linnaeus
Family COSSIDAE
Cossus cossus Linnaeus
Family TORTRICIDAE
Rhyacionia buoliana Schiffermueller

Family PHYCITIDAE
Dioryctria mendacella Staudinger
Dioryctria silvestrella Ratzeburg
Dioryctria pineae Staudinger
Family PYRALIDAE
Myelois cribrella Hubner
Family ARCTIIDAE
Tyria jacobaeae Linnaeus

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Book Reviews

Factors in the Distribution of Butterfly Color and Behavior Patterns—Selected Aspects.
Landing, Benjamin H., 1984. 200 pp. Published by the author; Los Angeles. (Available from Entomological Reprint Specialists, P. O. Box 77224, Dockweiler Station, Los Angeles, California 90007). Price: $17.95.

Revolutionary new ideas often appear unorthodox, radical, or controversial at first. In science this can create problems because of its inherently conservative, hard-boiled, skeptical nature, yet paradoxically science can only progress in quantum leaps via good new ideas (e.g., the microscope and telescope, evolution, relativity, continental drift). New ideas are often comparatively simple or simplify a problem and involve inventive, gap-bridging, or model-building abstract thinking. This book, written by a Harvard graduate in Entomology who is currently a medical professor was privately published to overcome journal rejection.

Landing has drawn upon his personal experience with butterflies on five different continents and the published literature. The common theme is "factors influencing the micro- and macrogeographic distributions of butterfly color and behavior patterns." The seminal paper by Papageorgis (1975, Amer. Sci. 63:522-532) is taken as the basis for his studies. Papageorgis found that *Heliconius* "mimicry" complexes were stratified by height in the Peru rainforest (from bottom to top: transparents, tigers, reds, blues, oranges), all subject to predation by the same birds but differing in light conditions. Not predicted by mimicry theory, cryptic rather than warning coloration was the rule.

What is new here is that Landing has applied Papageorgis's theory to the whole earth's surface and found these color classes drop out *in sequence* from low to high latitudes, i.e., transparents in Mexico, reds at the Canadian border, etc., thus indicating a tropical ancestry for butterflies, which dovetails with the fossil angiosperm data (paleo-hostplants) of Axelrod (1959). In essence, butterfly biogeography is largely dictated by the hostplants' biogeography (Jermy's 1976 sequential evolution), with the compliment of butterflies and vegetation being depleted in its spread to drier, cooler, and more seasonal climates in higher latitudes away from the tropics, during the Upper Cretaceous. Thus the number of butterfly classes present depends on the average height of the angiosperm vegetation in each area. Few other workers since the days of Seitz and Pagenstecher have considered the global laboratory of butterflies, most other accounts being far more provincial.

Extensive bird predation of butterflies is a not-often appreciated fact (see Remington, 1954, Lepid. News 8:31-43). Landing has succeeded in demonstrating a more fundamental relationship between bird predation and butterfly coloration-behavior than was heretofore supposed, again the result of applying Papageorgis's findings in an unexpected, worldwide sense. He has quantified much of his data for ease of comparison. Ch. 4 tests the general theory of butterfly distribution of color and flight patterns over the world against published data for the Sierra de Tuxtla, Mexico, and the Sierra Nevada, California, with a general concordance.

He assigns species to specific color/behavior classes from 0 to 5 based on upper-

side color, such as Class 0—brown species flying at ground-level. He also quantifies classes for size, habitat, dimorphic species, sun vs. shade, behavior, and geographic areas for analysis.

Landing notes that a disproportionately high number of butterfly species use mistletoes as larval foodplants probably because it confers distastefulness to avian predators of butterflies, as is known for Asclepiadaceae, Solanaceae, Passifloraceae, and Aristolochiaceae. Butterflies on these often serve as models for Batesian mimics. Protective coloration from mimicry or resemblance to leaves, bark, etc. transmits disinformation to predators. Chs. 7 and 10 are interesting, theoretical discussions of avoidance of distasteful butterflies by birds (visceral memory) and cryptic vs. advertising coloration, respectively.

A book of this nature is not without its faults. The chapters on butterflies seeing red colors and skippers as butterflies are inconclusive. He elaborately treats iridescence as protective interference coloration from avian predation, although it is sometimes thought to be a response to high rainfall. Ch. 8, a reconsideration of allopatric Batesian mimicry effected by migratory birds remembering patterns, is controversial, with examples and reasons both for and against it being presented.

His estimate of 20,000 world butterfly species seems too high. Owen (1971) gives 13,000 species, which tallies with my findings, and Hemming (1967) estimates 2,400 genera, or an average of 5 2/5 species per genus. This average compares well with birds, which have 4 4/5 species per genus (8,600 sp., 1,800 genera) (Mayr, 1946). This surprising similarity was early pointed out by Kirby (1872).

I do note a few important studies of color and pattern in butterflies that were not included, e.g., Nijhout (1981), Schwanwitsch (1924, 1929), Scott (1973), and Suffert (1927). Also, it is a pity that the important review by Pianka (1966) of concepts of latitudinal gradients in species diversity was not discussed. The tables and figures do help to follow his development.

The book should appeal to those interested in the evolution, mimicry, behavior, ecology, and biogeography of butterflies but may be intellectually beyond the layman's grasp because of the high degree of difficulty of the concepts.

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Factors to the Distribution of Butterfly Color and Behavior Patterns—Selected Aspects
Landing, Benjamin H., 1984. Published by the author. 200 pp. Price: $17.95.

The papers that constitute this work have two things in common. All have been presented over a number of years at meetings of the Lepidopterists' Society and all have been rejected in manuscript by journals. This is pertinent, for it assures us that the author has had feedback on this material, both in person and in review. Yet, despite that feedback, this self-published act of defiance remains as vague and convoluted as its title. Most likely, I am not the only one initially to think that the "distribution of a butterfly color" refers to the distribution of colors across wing surfaces, not to the distribution of butterflies of certain color combinations across habitats. Unfortunately, following this opening, Landing moves from ambiguous to muddled, and from there to out-and-out wrong. While that is grounds to dismiss the book out of hand, there remains, nevertheless, a methodological lesson to be

learned from this book. A good many competent butterfly biologists have simply dismissed the component papers on an individual basis and, it seems, no one has dissected out the faulty premises which form the foundation of Landing's mysterious melange of ideas.

> "That each butterfly species has the anatomic, biochemical and behavioral components of its particular 'butterflyness' inherited as a 'package,' with the components 'geared together,' is not a new concept, but, until in this century how this was effected, or how the components of the package developed as they did in the first place, could not be discussed analytically because of lack of fundamental biochemical and genetic concepts from which to derive a vocabulary adequate to the task."

Whew.

Landing then sheds light on the inheritance of behavior patterns, noting:

> "It is useful, however, in analyzing butterfly behavior patterns and the factors that influence them, to have an a priori opinion, in at least a general way, of what one includes in the concepts behavior pattern or program, of how many sorts there may be, and of what environmental factors one might expect to influence their survival value and development. The papers in this book address, fundamentally, this level of understanding, and are presented as back-ground, so to speak, or basis, from which more fundamental studies of the genetic and biochemical cellular mechanisms by which such behavioral programs are developed, modified and preserved can take off."

Landing apparently confuses the simplifying abstractions of models used by theoretical biologists with his arbitrarily uncomplicated view of ecosystems themselves. The purpose of the former is to aid in thinking about phenomena, processes, rates and such, and to generate predictions that can be tested in the field. Landing uses his model of sorts to explain observations already in hand. Thus his exercise is circular, since no alternative explanations for phenomena are entertained, much less tested. The roots of this exercise are reminiscent of the controversial work of Papageorgis (1975, Amer. Sci. 63: 522-532) which documented the partitioning of tropical forest into flying-height zones by distinctly-colored butterfly mimicry complexes. But Gilbert (1984, Chapter 3, *The Biology of Butterflies,* Academic Press) has discussed how that particular study (in contrast to those of Landing) has encouraged others to examine microhabitat separation in more detail.

Further considering the absence of scientific method in Landing's work (and, therefore, why it will fall to act as a "take-off" point for future studies), we should explore his basic premise, which he calls the "concept of ecological niches of flying butterflies." That concept, unfortunately, is the thread that ties together this collection of papers. This is unfortunate because "ecological niche" has a generally accepted formal definition in biology: it is "the sum of all the environmental factors acting on an organism" (Hutchinson, 1944, Ecology 25: 3-26). There is no such thing as a "flight niche" *per se*. Nonetheless, Landing contends that available "behavioral niches" (apparently synonymous with ecological niches) for butterflies exist that have as their "dimensions": (1) the color of a butterfly; (2) its size; (3) its "locus" of flight; and (4) the geographic regions of the world. Just these four components supposedly allow us to understand why butterflies of given colors are found where they are found. Landing says that eight colors of butterflies are defin-

able (viewing dorsal wing surfaces only), that butterflies are of three (or four) sizes, that they fly in three types of habitats (open, shade and edge), and that this happens in seven regions of the world.

You are probably getting ahead of me here. Yes, that means we have 8 x 3 (or 4) x 3 x 7, or some 500 or 600 or so, "behavioral niches" for butterflies on earth. Then again, he does suggest that there might be 4 or 6 colors, 1 or 4 sizes, or 6 habitats, or 5 or 6 regions, or any permutation of the above. Thus, there are some "147 to 1008 theoretically available behavioral niches in the world," into which some 20,000 species are distributed.

Now, ignoring the near order-of-magnitude noise in the "system" above, you might ask, as I did, what exactly this exercise allows one to do. I am afraid the answer is, not a doggone thing. Landing, nonetheless, spends some 200-odd pages carving up butterfly faunas into oddly arranged color "complexes" and dividing habitats into specific depths, heights, and layers, ultimately telling us that (except for hesperiids, "bark-colored American nymphalid butterflies," dusk-flying South American brassolids [sic], etc.) most butterflies fly where they should, and that is why we won't find *Morpho sulkowski* in Fort Dawson.

Actually, Landing says we find fewer color classes because there are fewer "behavioral niches" as we move away from the equator toward ecosystems with decreasing vertical structure. A welter of exceptions are noted, but, all in all, we are told that "the scheme accounts for the well-known fact that the number of species found at a specific site is greatest in the tropics." Accounts for? Well, not really, since that very information was put into the exercise in the first place. Thus, this scheme does not account for or explain anything of the sort. I agree that as one takes samples along meridians from the equator to the poles one loses "color classes" and size classes, as well as diversities of shapes, numbers of tails, sizes of eye spots, iridescence and on and on, as butterfly diversity decreases along with biotic diversity in general. Landing does not, however, tell us why that happens; he only tells us what we already know, *that* it happens. Oviposition host selection and breadth, the role of nectar as a limiting resource, the use of alternative sources of carbohydrates and amino acids, thermal constraints on butterfly activities, how resources are partitioned, how butterfly diversity and plant diversity correlate and so on, are all superfluous to Landing's construct. Apparently in the name of simplification, Landing has overlooked the vast majority of factors well-documented as playing roles in determining butterfly population and community structure.

The large number of tables and graphs throw something of a smokescreen to conceal Landing's unscientific procedures, but the final chapter, "On Seeing Red", clearly demonstrates how he generates his theories. Without a shred of new supporting evidence, he suggests that butterflies probably see the color red because the color is common on butterflies, particularly on those in mimicry complexes. Landing combines that with the observation that some butterflies visit red flowers and has a solid case from his peculiar point of view. But the best evidence for butterfly vision in the "visible" red portion of the spectrum is ignored by Landing. Studies have not only shown hue discrimination in that spectral range; they have demonstrated a concordance of butterfly wing colors and peak neural responses (that is, red butterflies particularly respond to red and green butterflies to green) as well as a communication function for the color red (see various papers by Crane, Swihart, and others).

By itself, however, attraction to a member of the opposite sex with red wing markings or visitation to flowers with red markings on their corollas are far cries from usually perceiving red as a color. Certainly my well-developed skill at spotting certain daisies with white corollas or *Colias* butterflies with yellow wings does not indicate that I am blessed with the ability to see the dramatic ultraviolet patterns we also know to be present. In fact, the frequency of red patterns in mimetic complexes suggests that the color serves to warn vertebrates that we know can see the color red to avoid those butterfly species. For species in mimicry complexes, nonvisual mating cues may predominate because the recognition of conspecifics is confounded by the presence of other visually similar species. As pupal mating in some *Heliconius* and the clear-winged adults of some ithomines bear witness, all colors may be superfluous in mate recognition for such groups. The existing experimental evidence that suggests otherwise, again, is not cited by Landing.

This book very simply lacks any scientific rigor whatsoever, from its lack of testable predictions, to its paucity of alternate explanations for observations, to its absence of supporting literature citations. Now, arguably, the good news about this book is that since it was published by the author, circulation should be limited. The bad news is that some clearing houses for scientific books are already listing it. Butterfly enthusiasts lacking formal training in biology will be attracted to that rare commodity—a reasonably-priced book about butterflies. They well may assume that Dr. Landing is actually onto something. In fact he only shows how far from modern biology much work on butterflies remains.

This volume does stand as a grand counter-example to the old saying that one should not judge a book by its cover. This book is about butterfly color; its cover is black and white. That seems appropriate.

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Lepidoptera: Hesperiidae. Notes on species-group names.
Bridges, Charles A., 1983. Available from the author, 502 W. Main Street, Apt. 120, Urbana, Illionis 61801, U.S.A. Price: $35.00 + $2.50 shipping

Sooner or later every taxonomist sighs for a catalogue of all available names in his beloved group, and many a one may even have toyed with the idea of making such a catalogue himself. Even with the help of modern computers this is, however, an immense task if the group under consideration has some size. We must therefore be very grateful if somebody undertakes such a work. The present catalogue gives even more than a list of names and we can but welcome its publication.

The main part of the work (129 pages) is a list of all species-group names (in the sense of the International Code of Zoological Nomenclature) of Hesperiidae, with original combination, authorship, year and place of original publication, current usage, location of type specimens, references, occasional brief notes, and indications of availability and validity. The main source for the determination of current usage has been the well-known catalogues by Evans (1937-1955), whereas later described taxa are given the same rank as in the original publication. No original work on Hesperiidae has been done by the author, and no new names have been proposed. The list is, thus, a compilation from the literature. The extent of

work involved in compiling this list can be grasped by realizing that more than 9,000 names had to be dealt with. Currently 3,498 species are recognized (i.e. were recognized in 1982) of which about two thirds are monotypical. About half of the recognized species were described in the second half of the 19th Century. In the last 25 years about 12 species were described as new each year, indicating that our knowledge of the Hesperiidae is still far from complete.

The second part (41 pages) is an alphabetical index to the 532 genera currently recognized. Under each genus an alphabetical list of species, subspecies and synonyms is given with author's names, year of original description and original combination. Since the catalogue deals with species-group names only, it is not surprising to find that no information is given on authorship and year of the genus names nor on the type-species. For the names up to 1967 this information can, of course, be found in Hemming (1967), with additions by Cowan (1968, 1970). Inclusion of this information in the present volume would have taken little room and have made the catalogue even more useful.

In the third part (62 pages) the authors and their publications are enumerated, with a list of the new species-group names per publication. In many cases biographic notes on authors are added. This part serves as an index to the fourth part (30 pages), the bibliography, which includes 1,640 citations.

The fifth and last part (13 pages) is an index to more than 250 journals and serials where the new descriptions have been published, with full titles, World List abbreviations, and notes on the dates and places of publication. Under each journal or serial a list is given of authors of new names with dates of publication and further bibliographic references.

The wealth of information and the various entries to it makes the work indispensable for any serious taxonomist working on Hesperiidae, and most useful to anyone generally interested in butterfly nomenclature. The catalogue does not supersede Beattie (1976). The latter is only an index to all literature on butterflies recorded in the Zoological Record. Taken together however the two works provide a source of information earlier students could only dream of.

It is almost inevitable that there are omissions in a work of this size. Indeed, a few publications have been overlooked. Such omissions can, however, easily be remedied if everyone working with the list informs the author of additional names. The list is obviously incomplete where the location of type specimens is concerned, since this data has not been taken from the original descriptions but mainly from Evans (1937-1955) who only mentioned the location if the type was in the British Museum (Natural History), with a few exceptions, and from Miller & Brown (1981) who cover North American species only. Completion of this information would be most welcome, but will certainly need the co-operation of many people.

Finally a minor point of criticism. If the original combination of genus and species name is different from current usage, the author's name, but not the year, has been placed in parentheses. This is not in accordance with Recommendation 22B of the International Code of Zoological Nomenclature which reads as follows: "If the original date of publication is cited for a species-group name in a changed combination, it should be enclosed within the same parentheses as the name of the original author".

In short, this publication is a major reference work for species-group names in

Hesperiidae. Every entomological library should have a copy. It is moreover strongly recommended to all students of skipper taxonomy and other people interested in butterfly taxonomy in general. We can only hope that the author will find time to produce similar catalogues for other butterfly families.

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The Audubon Society Handbook for Butterfly Watchers
Pyle, Robert M. New York: Charles Scribner's Sons, 1984. 274 pages, hardback. $16.95

For several centuries the study of butterflies has focussed on the hunting and gathering of specimens and the making of collections. The situation remains much that way today, with most amateur naturalists who are interested in butterflies amassing assemblies of well-curated, dried specimens. Indeed, to the degree that amateurs have contributed to the knowledge of butterfly biology, it has often been as a sideline of collecting—identifying the habitats and phenologies of rare species and determining foodplants so that perfect specimens may be reared.

Both of us were butterfly collectors in our youth and still enjoy the hunt of elusive species and take pleasure in a fine collection. But we also have grown to enjoy observing and experimenting with living butterflies, an activity that evolved naturally as we became professional biologists. This leads us to ask, why does collecting alone still dominate the interests of amateur lepidopterists? One reason, we think, is that collecting dominates the texts, handbooks, and field guides on butterflies. Unlike birds that must be watched (few birders are permitted to collect them anymore), butterflies can be studied in hand—so the natural focus has been on getting them there.

Bob Pyle's new book may be a step toward changing attitudes about collecting. Here we have a guide that encourages people to think of butterflies as living organisms first and pinned, labelled drawer-fillers second. Pyle's mentor, Charles Remington, encouraged such a shift of emphasis in the late 1940's when he

published a series of articles in the early volumes of the *Lepidopterists' News*. Topic titles included "The important of life history investigations", and "Lepidoptera biology—open for study." Pyle has followed this lead, creating a manual on how and where to watch live butterflies.

The book coaches the butterfly watcher in how to find and rear butterflies, record scientifically valuable notes, and contribute to our understanding of their diversity and abundance with simple quantitative assays of populations. The "how to" sections range from butterfly gardening (euphemism for allowing weeds and *Vanessa* to take over) to butterfly photography to unquestionably the most important facet of butterfly biology at present—their conservation, along with that of their often threatened habitats. In the chapter titled "Great North American Butterfly Spots", Pyle almost (but not quite) tells us exactly where those spots are.

All this may sound like the last book that the well-versed butterfly biologist and Lepidoptera addict might need or want. Most of us, however, are more often surrounded with interested innocents than empathetic colleagues. For that larger group, this is the book. And, while this well may be the perfect beginner's guide, the evocative images and piquant observations make enjoyable reading for even the most intense butterfliers. The book is unquestionably well-written; the author's prose however, will not be to everyone's taste—"purplish coppers doing an allemane-left", "besotted red admirals", "french vanilla females", and pine whites going "mad for blue lobelias". Larvae don't just pupate, they "roll leaves into snug sleeping bags" becoming "sarcophagi for the dead season" after which "the mummy case[s] burst open". What emerges may be Uhler's Arctics (which even we could translate into a recognizable binomen) or Whirlabouts (we're still working on that one!).

If we were to have any serious criticism of the book, it is that we wish that Pyle had gone into even deeper detail on the *why* of watching live butterflies. Besides providing great personal pleasure, this activity is now contributing to our knowledge of the ecology and behavior of a group of organisms that has become a model for understanding how nature works. Pyle does indicate this, but we would hope that the book will be so successful that in a revision he may give even more explicit directions to amateurs who wish to combine the pleasure of butterfly watching with making effective contributions to the understanding of the world around us.

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The World of Butterflies and *Il mondo delle farfalle.*
Sbordoni, V. & S. Forestiero, 1985. Blanford Press, Poole, Dorset, England. 312 pp., 111 col. pls., numerous line drawings. Price: 20 Sterling Pounds. (Translated from an Italian book "Il Mondo delle Farfalle" published by A. Mondadori, Milano, Italy; lit. 50.000).

It is extremely difficult to strike a balance between the popular and the scientific, to write a book attractive to both the scientist and the layman. E. B. Ford ("Butterflies") once accomplished this task with a remarkable success. Now Sbordoni and Forestiero managed to do at least the same all over again. Although their topic

must be seen as even more pretentious, they have written a book which is useful to the scientist studying Lepidoptera and at the same time can be read from the first to the last page by a layman—and understood by both. The text consists of the following chapters: Foreword; Preface; Structure, Origin and relationship of butterflies and moths; Life cycle and metamorphosis; Diversity and evolution of butterflies and moths; Origin of species; Systematics: classification and phylogenetics; Systematics of butterfly and moth families; Behaviour; Ecological relationships; Strategies against predation and mimicry; Ecological distribution; Geographical distribution; Butterflies and man; Classification of Lepidoptera; Catching and preserving Lepdioptera; Conservation of Lepidoptera and their environment; Bibliography; Index. The color illustrations (from watercolor originals) are instructive, but somewhat "artistic" and "showy", though usually extremely well chosen to demonstrate the desired process (e.g. predation by birds and reptiles: pp. 196-201). The technical standards of production are good, as usual in Italy. A further plus is the modern concept and inclusion of up-to-date methodology, such as the description of electrophoretic studies (p. 84). The book under review deserves much praise, but cannot be considered faultless. For instance some phylogenetic conclusions left me unconvinced and the blue figures on plate 69 are *Polyommatus bellargus* (misidentified in both the Italian and the English edition as *P. icarus*). Further, the English translation of the title is wrong: the Italian word "farfalle" means butterflies *and* moths! It is certainly a great pity that the authors chose to follow the contemporary "splitting" of many genera (e.g. *Cynthia, Mesoacidalia, Lysandra, Plebicula,* etc.), a choice particularly unfortunate because this book is very likely to become widespread in both professional and amateur entomological circles. Nonetheless, the authors have produced an exceptional book and deserve cordial congratulations. I strongly recommend the book to every butterfly student and collector, it will help him learn and understand the science of lepidopterology. The book is also reasonably priced and does not sport the infamous "D'Abrera Effect". The Italian edition is printed on better, heavier quality paper and probably better bound, too; otherwise the number of pages and illustrations is the same in both editions. The publishers would be well advised to produce a German translation.

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Generic Revision of the American Zygaenidae, with descriptions of New Genera and Species (Insecta: Lepidoptera).
Tarmann, G., 1984. In German. Supplement 1-2 of Entomofauna. 176 + 153 pp. Linz, Austria. Size: 6 x 8½ in. Sales: Tiroler Landeskundliches Museum, Zeughausgasse 1, A-6020 Innsbruck, Austria. Price: $25.00 U.S. (600 Austrian Shillings), include $1 surface or $4 airmail.

This new work is a much needed revision of all the New World moths of the family Zygaenidae, the so-called smoky moths or leaf skeletonizer moths. The work is divided into a text part and an illustrations part, the latter with 438 black and white photographs or line drawing figures; both parts are hard bound as one book. The revision covers the single subfamily Procridinae that occurs in the New World,

with 24 genera and 156 species from North and South America. There are 5 new genera and 24 new species described in the book, plus many new combinations and new synonymys. The introductory part covers taxonomic features and history of zygaenid moths, general distribution, biology, host plants, and behavior. There also is a paragraph on the curious cyanide resistance of many zygaenids, one species from Guatemala being noted as unaffected by cyanide after even 30 minutes in a cyanide collecting vial. A checklist and keys to taxa are also provided. The illustrations show the adult moths, detailed morphological features, wing venations, and genitalic characters. Although the text is in German, the illustrations and geographic distributions provided allow anyone to identify New World Zygaenidae using this book. Most of the new species are Neotropical but 4 new species are described from the United States. The revision appears to be a very thorough and detailed job, the author having studied many museum collections as well as having conducted personal field trips to the eastern United States, Mexico and Guatemala. This book will be needed by anyone interested in these unusual moths and the price will easily allow this also.

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Notes

Natural History Notes on *Brassolis isthmia* Bates (Lepidoptera: Nymphalidae: Brassolinae) in Northeastern Costa Rica

In this note I summarize observations on the larval natural history of the butter-fly *Brassolis isthmia* Bates (Lepidoptera: Nymphalidae: Brassolinae) in northeas-tern Costa Rica. The gregarious habit of the caterpillars and their associated tent-building behavior make this species an interesting one for further study. This note extends some of the detailed Panamanian observations made by Dunn (1917) for this species to Costa Rica. The genus *Brassolis* is composed of four species (Fruhstorfer, 1924) of which *B. isthmia* represents the group in Central America and Colombia.

The study site is "Finca La Tirimbina" near La Virgen (220 m elev.), 10°23′N, 84°07′W (Heredia Province), within the Premontane Tropical Wet Forest Zone (Holdridge, 1967). A group of *B. isthmia* caterpillars was studied from 8-11 July 1982 in this locality and subsequently by rearing them in captivity through pupa-tion and eclosion. Field observations consisted of determining diurnal feeding periods over three successive days for caterpillars as well as noting defensive behavior. Once they had been collected for rearing, descriptive (morphological) notes were taken on the caterpillars and pupae. A determination of the food plant was made along with noting the patterns of defoliation, presence of previously occupied communal nests, and association of caterpillars with the presently-occupied nest. Samples of the caterpillars, head capsules, pupal cases, and adults have been deposited in the collections of the Milwaukee Public Museum.

A second group of caterpillars discovered on the same tree on 29 February 1984 were used to test the idea that *B. isthmia* can successfully switch from *Chaemodora* palm to *Cocos* palm as a food plant. The ten caterpillars were found in a single tent on the *Chaemodora* and transferred 10 days later to *Cocos.* Obser-vations were then made on feeding and survival of the caterpillars.

Ten caterpillars formed a single communal nest on the food plant. Most were 60-65 mm long with maximal width of head capsule (left-to-right axis) being 7 mm. Head capsule shiny black and covered with short, scattered white setae (Fig. 1). Three small white spots on each side of the head, adjacent to mandibles. No red markings of the kind reported by Fruhstorfer (1924) for the related *B. astyra* Stick in Brazil. Head suture reddish. General background color of body reddish-brown. Basic color pattern complex series of longitudinal (lengthwise) stripes of varying thickness and intensity of color. Thin dorsal-medial faint yellow line bordered on each side by thicker red-brown line, followed laterally by thick cream-colored line to either side, speckled with dark red flecks. Laterally with very thick area of the background color. Same dorsal pattern of stripes repeated once on each side of body. Ventral area and prolegs reddish. True legs black. Rounded anal plate brown with body segment anterior to it with simple stripe pattern of medial dark red line bordered with white. Same color pattern occurs on "neck" region. Entire body covered with sparse covering of short, whitish setae. Further details of general dis-tribution of setae given for *B. astyra* from Brazil by Fruhstorfer (1924). As reported by Fruhstorfer, overall body profile cylindircal with middle region thickest, taper-ing near ends, and with frontal view of head capsule broadest at base and tapered
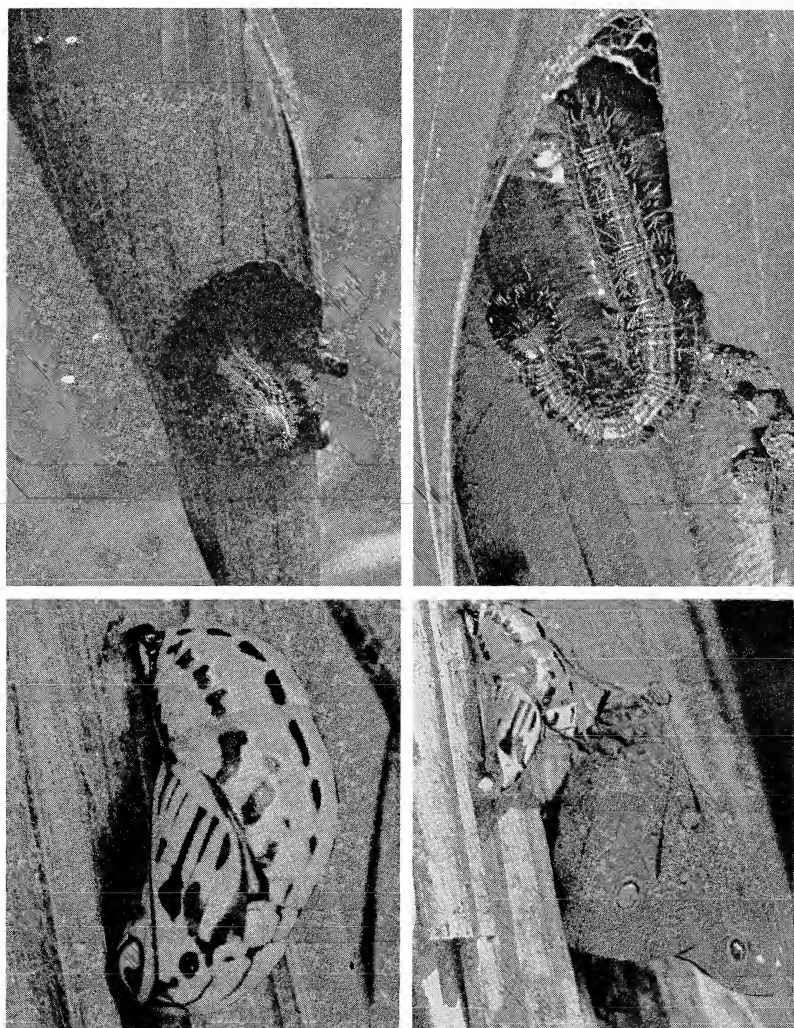
Fig. 1.   Clockwise, from top left: _B. isthmia_ caterpillar protruding from opening at distal end of nest; final instar caterpillar; pupa; adult eclosion.

dorsally. A partial description of the early stages of _B. isthmia_ is given in Dunn (1917).

In captivity the caterpillars grew to about 70-75 mm before contracting to short mobile prepupa stage exhibiting no changes in color. Active prepupa about 40 mm long.

Pupa stout and thick, 23 mm long and maximal dorsal-ventral width 11 mm (Fig. 1). Ground color varying shades of yellow and light pink, with black markings and

black cremaster. Abdominal area with prominent pair of ventral black spots. Black spiracular markings adjacent to reddish spiracles. Dorsal-lateral pair of thick black spots comprising a longitudinal band; also other similar bands medially and more dorsally in same manner (Fig. 1). Thin border of pale yellow arises between ventral-lateral and lateral black bands, followed by thicker band of pink and thick band of deep yellow in dorsal area. Thin alternating bands of faint pinkish-white-to-pink-to-faint-pinkish-white tinged with yellow-to-pink-to-faint-pinkish-white found between the lateral and dorsal-lateral black longitudinal bands. Between the dorsal-lateral and dorsal (medial) longitudinal black bands a series of alternating colors: thin line of pale yellow-to-thick pink band-to-thin border of pale yellow. On second, third, and fourth abdominal segments blackish-brown splotches interrupt yellow areas between the lateral and dorsal-lateral black bands. These paired splotches largest on third segment and smallest on fourth. Each wing pad

Fig. 2. Caterpillar nest for *B. isthmia*. Left: dorsal view; right: ventral aspect.

yellow and streaked with rusty reddish-brown lines which coalesce into large triangular splotches of same color near base of each wing. Large roundish spot of same color where wing joins thorax. Dorsal area of thoracic region light pink with medial and lateral think rusty-brown lines (lengthwise). Antennal and leg areas yellow and marked with light rusty-brown lines and spots. Head area yellow with large dorsal-ventral band of dark brown; area of compound eyes bisected into yellow (posteriorly) and dark brown smaller area (anteriorly); palps area deep yellow. Antennal cases sometimes pinkish instead of yellow. Pupa hangs pendant and darkens considerably within a day of eclosion. Final molt to pupa takes 1-2 days. Duration of pupa stage (N=5): 14 days (at about 28°C). Dunn (1917) noted that the pupal stage for this species in Panama lasts 14-17 days. Eclosion requires about 20 min (Fig. 1).

The caterpillars were discovered on a 3 m tall palm tree (*Chaemodora* sp.) growing alongside a small house in a forest clearing. The tree, one of several planted near the house, had been planted as an ornamental at least ten years prior to the discovery.

During the daylight hours, the caterpillars stayed inside a silken tent-like structure (Fig. 2) fashioned by weaving together the pinnae of a single palm frond. The inner surface of the "tube" was lined with thick brown silk. The tube was about 35 cm and 9 cm wide at the middle region. Near the distal end the caterpillars chewed a large opening from which usually 1-2 individuals could be spotted partly exposed during the day (Figs. 1-2). The tent-nest was constructed by anchoring together, in a very orderly manner, the edges of the pinnae curled downward to the axis of the fronds (Fig. 2). The pinnae thus attached remained lush and did not wither. No structural damage to the pinnae or fronds was apparent. There are copious amounts of the silk extending down the fronds to the trunk area of the tree. The opening at the distal end is partly covered with a thin sheet of silk, whereas the proximal area is open and unobstructed. The caterpillars rest on the silken carpeting inside the nest, and all face with heads towards the distal end. Gentle squeezing of the tent did not produce noticeable movement or exodus of the caterpillars. The distal area of the nest, at the time of discovery, contained large accumulations of grass and two dead caterpillars. But large nests in coconut palms in Panama are often open at this end, allowing free passage of fecal matter to the ground (Dunn, 1917).

When prodded with forceps, the caterpillars with head capsules exposed at distal opening of the nest (Fig. 2) reacted defensively in attempting to bite the forceps. The caterpillar possesses a ventral glandular opening just anterior to the prothoracic legs. This structure appears similar to that found in the caterpillars of *Morpho* (A. M. Young, unpubl. data). No noticeable odor was detected, however, when the caterpillars were disturbed.

A striking behavioral feature of larvae was their crepuscular feeding habit. On the three evenings of study, all of the caterpillars exited from the nest in unison between 1710 and 1730 hours (i.e., about 1 hr after sunset), and fed for approximately 45 min before returning in unison to the nest. The caterpillars leave the nest one by one, forming a line and crawling to another frond for feeding. Two of the ten caterpillars were considerably smaller than the others, although their feeding behavior did not vary.

One of the fronds used for feeding had an old and abandoned nest, and this section of the leaf was not fed upon. Another frond had another abandoned nest of

similar size. During one feeding period (9 July), four caterpillars lined up on one pinna to feed, two on an adjacent one, and two more on another pinna of the same frond. As reported for *B. astyra* by Fruhstorfer, a loud clicking noise could be heard as the caterpillars fed. Checks at other times of the day, including the period of 0500 to 0700 hours, revealed no feeding activity by the caterpillars, indicating that they feed just after dusk each day. Caterpillars always leave and reenter the nest from the proximal end. Although Dunn (1917) reported tha the caterpillars feed only at night, I would modify this statement somewhat by suggesting a crepuscular feeding habit, i.e., one in which there is a brief feeding period about an hour after dusk. The same palm tree contained active nests of two different social paper wasps (unidentified polybiines) and o interactions with the caterpillars were observed.

During the daylight hours of the third day of study, I checked the "feeding" fronds for signs of silken trails but could find none. I deliberately rubbed my hands over the stems of the fronds involved, including the one with the nest. When the caterpillars exited that evening, they exhibited "confused" and disoriented behavior. Three caterpillars quickly crawled to the fronds used for feeding. The remaining six followed suit only part way, but then reversed their direction and went back down the stem. Three individuals began feeding on a pinna near the tip of the fronds, and another two at a basal pinna. Another caterpillar returned immediately to the nest without feeding and remained inside for about five minutes before exiting again. Three others crawled to a different frond but eventually turned around and joined up with the one (see above) leaving the nest for a second time. Threse four caterpillars then went back to the original fronds used for feeding on previous days. The tenth caterpillar was unaccounted for and possibly missed during the tracking observations. When crawling, each caterpillar characteristically arches its head upwards and waves it from side to side. Further observations of behavior of caterpillars, in different instars, is given by Dunn (1917).

Rearing was accomplished by placing the entire fronds bearing the nest in a large clear plastic bag, adding an additional frond, and keeping the bag shut. The caterpillars continued to exhibit the same diurnal feeding pattern in captivity as on the tree. Pupation sites varied considerably in the bag, with two being on the silken mat near the proximal end of the nest.

When transferred to *Cocos*, third-instar caterpillars fed successfully and pupated. Such an observation suggests some feeding flexibility in *B. isthmid* caterpillars for feeding on various Palmae.

Brassolis (Fig. 3) is one of two genera that very characteristically lacks the prominent bifid tail so diagnostic of caterpillars of several other brassolid genera (Fruhstorfer, 1924). Both the related Satyridae and Morphidae have caterpillars with bifid tails, a character often used to link these groups (e.g., Miller, 1968).

Fruhstorfer (1924) described the egg, final instar caterpillar and "bag" nests of *B. astyra* in Brazil. He reported that the larval period in this species lasts 7-8 months, a period similar to that of *Morpho* (Young and Muyshondt, 1972). Both Jones (1882) and Fruhstorfer (1924) report that sometimes several hundred caterpillars of *B. astyra* occur in a single nest. Larger nests and great numbers of caterpillars per nest are known for *B. isthmia* for the Limon region of Costa Rica's Caribbean rain forest lowlands. Dunn (1917) reported egg masses for *B. isthmia* ranging from 150 to 300 in Panama. Dunn also found from 50 to 2000 caterpillars in a nest.
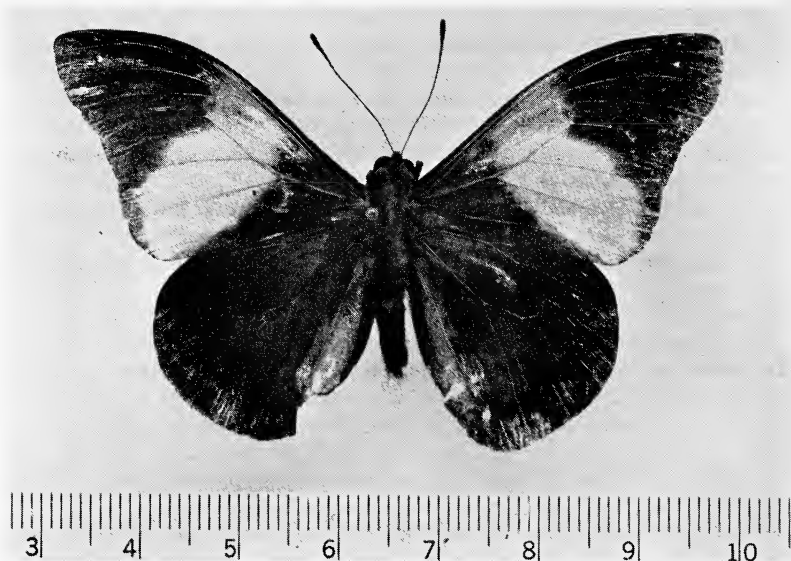
Fig. 3. Adult *B. isthmia* (male) reared in this study.

Like other brassolids such as *Opsiphanes*, adult *B. isthmia* are markedly crepuscular in habit, with reproductive behavior confined to the dusk period (see also Young and Muyshondt, 1975 and Young, 1977, for *Opsiphanes*). Jones (1882) noted that pupation in *B. astyra* occurred away from the nest, while Fruhstorfer (1924) reports pupation within the nest. Dunn (1917) reported pupation outside the nest for *B. isthmia* in Panama, where high numbers of caterpillars per nest have been found in coconut palms. Under conditions of low density, some pupation may occur within the nest (Fig. 4).

Various authors (Jones, 1882; Fruhstorfer, 1924; Brown, 1972) have commented upon the cycling of brassolid broods in South America. In more than a decade studying Lepidoptera at La Tirimbina, the data reported here comprise the first set of observations on *B. isthmia*. The butterfly may exhibit seasonal cycles of abundance even within a relatively non-seasonal area like northeastern lowland Costa Rica, a factor contributing to its apparent scarcity at this locality. Seasonal cycles of abundance in which there are two, somewhat overlapping broods each year have been noted for *B. isthmia* in Panama, where this butterfly has been a defoliator of coconut palms (Dunn, 1917). In the Limon area, the butterfly is commonly associated with very large palm trees, suggesting a lower understory habit within natural rain forest. In close to ten years of bait-trapping many brassolids on the ground cover of rain forest in this region of Costa Rica, I have never captured *B. isthmia*. The butterfly might be more active in upper layers of the forest than near the ground.

Both the cryptic coloration of the caterpillars and the dusk-feeding habit suggest a passive defense against natural enemies. The function of the glandular opening

near the prothoracic legs remains unknown. Whether or not the function is associated with defense or with establishing an odor trail used in communal feeding and nesting habits remains to be studied. During the larval period, several different nests might be used on a single food plant, as suggested by the occurrence of
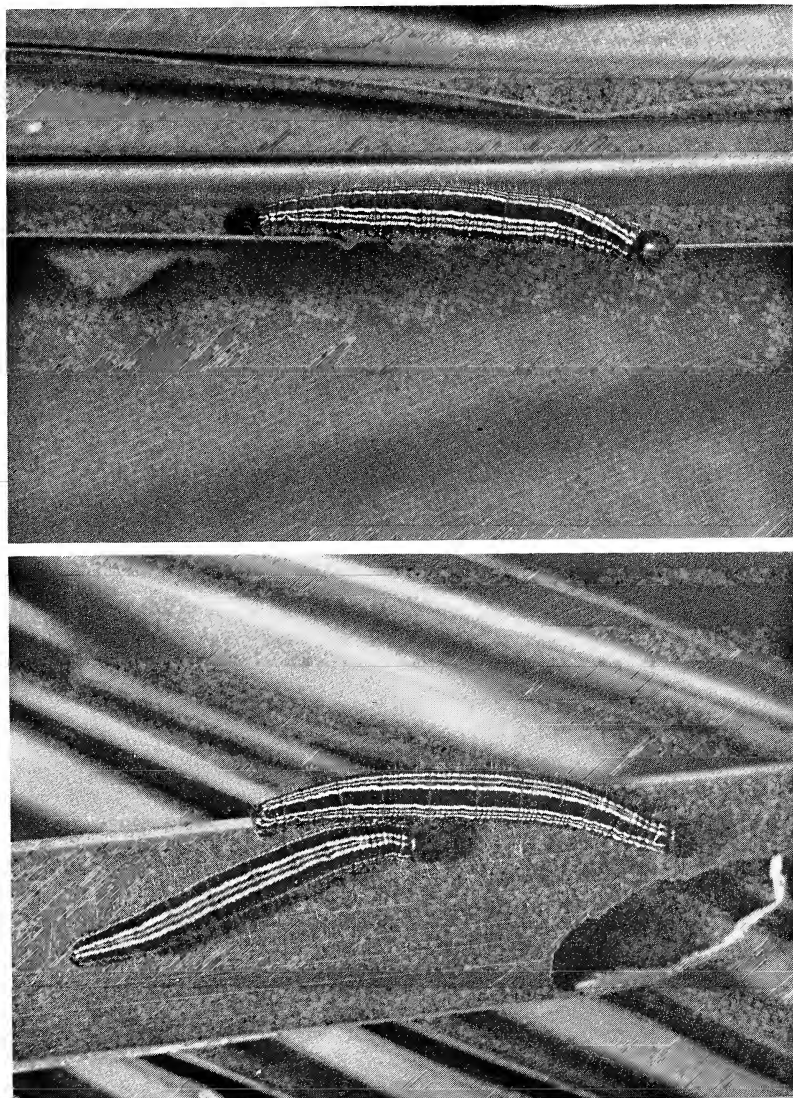

Fig. 4. Above: single final-instar caterpillar searching for pupation site; below: two fifth-instar caterpillars preparing "communal" pupation site on fronds of food plant.

two unoccupied nests on the palm under observation in the present study.

I thank Dr. J. Robert Hunter for showing me the caterpillars on the palm tree next to his home at La Tirimbina.

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Moss-Feeding by a Satyrine Butterfly

A previous paper (Singer, M.C., P. R. Ehrlich and L. E. Gilbert, 1971. Butterfly feeding on Lycopsid, Science 172:1341-1342) gave the first report of butterflies using lycopsids as larval hosts. *Euptychia jesia* (misidentified in the paper as *E. westwoodi*) was found to feed on *Selaginella horizontalis* in Panama. Since that time one of us (MCS) has found three other species of *Euptychia*, including the real *E. westwoodi*, to be host-specific on particular selaginellas in Costa Rica. We report here what we believe to be the first observation of moss-feeding by a butterfly. At Corcovado National Park, Costa Rica, *Euptychia insolata* was observed alighting on green tree trunks in oviposition search mode. We found six green spherical eggs and subsequently observed oviposition on the epiphytic moss *Neckeropsis undulata*. From the six eggs we were able to raise five adults on this host. We do not know whether other hosts are also used. The larvae of *E. insolata* are extremely cryptic, being both moss-shaped and moss-colored. A photograph of one on its host, taken by L.E. Gilbert, has been used as an example of camoflage in a general biology text (page 9 in Purves, W. K. and G. H. Orians, 1983: Lifre, the Science of Biology. Sinauer). We suspect that many of the South American Euptychiines will eventually be found to feed on "lower" plants.

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Occurrence of Homosexual Mating Pairs in a Checkerspot Butterfly

Male-male courtship is known in many organisms. It has been explained in terms of a low threshold for sexual attraction in general, such that males (but not females) produce courtship behavior in response to inappropriate stimuli (Symons, 1979, The Evolution of Human Sexuality, Oxford Univ. Press, NY). Others have discovered specific adaptive roles for male-male courtship. Male scorpion flies mimic females in order to steal prey items (Thornhill, 1979, Science 205:412-415); salamanders do likewise to interfere with mating by rival males and trigger the deposition of the rival male's spermatophore (Arnold, 1976, Zeitschrift fur Tierpsychologie 42:247-300). Lloyd (1979, Florida Ent. 62:17-34) found that bedbugs inject sperm into other males and that these sperm may be subsequently used to fertilize females. On the other hand, Acanthocephalan worms pass no sperm, but one male plugs the genital aperture of the other and renders it incapable of mating (Abele & Gilchrist, 1977, Science 197:81-83). Apparent courtship among male mammals is often interpreted as a dominance interaction, as in Mountain Sheep (Geist, 1971, Mountain Sheep: A study in Behaviour and Evolution, Univ. of Chicago Press, Chicago, IL).

Apparent courtship among male insects usually does not lead to copulation (Frias et.al., 1984, Ann. Entomol. Soc. Am. 77:548-551). In butterflies, male-male aerial interactions are common, but are not usually described as courtship, although Rothschild (1978, Antenna 2:38-39) has described an incident of "rape" by a male *Danaus plexippus* of a male *D. chrysippus alcippus*, with resulting injuries to the "raped" individual. Her observation was made on captive butterflies; we know of no such accounts from the field apart from our own, reported here. While gathering mating pairs of the nymphaline, *Euphydryas editha* at Generals Highway, Fresno Co., California, (described in Rausher et.al., 1981, Anim. Behav. 29:1220-1228) we have found pairs of males lightly joined together, sitting back to back, in the characteristic pose of mated heterosexual pairs. In 1984, we found six male-male pairs, and 145 heterosexual pairs. Unfortunately, we cannot use these figures to estimate the frequency with which homosexual mating occurs; to calculate this, we need to know the mean durations of male-male and male-female matings. Homosexual courtship is frequent, and almost always involves an attempt by a mature male to mate with a teneral individual. If 'mating' occurs, the genitalia of the mature male grasp the teneral male in the position where its genital aperture would be if it were female. It is possible that the teneral male is injured or sterilized. Of the six teneral males found mated in this way three would not court teneral virgin females (tested repeatedly over a four day period) and three mated but only two of the matings were fertile. These data are not sufficient to estimate effects of homosexual mating on fitness. Since we have not found sufficient male-male pairs in the field for controlled experiments, we are now using captive males which readily duplicate in the greenhouse the behaviors we have described. Our preliminary results show that 'raped' males are not plugged.

We would be grateful for reports of similar behavior from other entomologists, as we hope to understand it in terms of its relationship to other aspects of butterfly courtship (Rutowski, 1982, Florida Ent. 65:73-82; 1984, J. Res. Lep. 23:125-142).

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Description of the Larvae of *Coenonympha haydeni* Edwards (Lepidoptera: Satyrinae)

The satyrine genus *Coenonympha* is represented in North America by two species complexes; one contains only *C. haydeni*, a primitive species without any close relatives, and the other, *C. tullia* contains six subspecies: *C. tullia california, C. tullia ampelos, C. tullia kodiak, C. tullia ochracea, C. tullia inornata* and *C. tullia nipisiquit* (Davenport, 1941, Bull. Mus. Comp. Zoo. 87:213-350). Although the larvae of species in this genus are easily reared in the laboratory, nothing is known about the early stages of four out of the seven North American groups, and only brief descriptions exist for the other three subspecies (*C. tullia california*— Comstock, 1927, *Butterflies of California*; *C. tullia ampelos*—Edwards, 1887, *The butterflies of North America*; *C. tullia inornata*—Davenport (loc. cit.), and Brown, 1961, Can. Ent. 93:107-117). The purpose of this report is to describe the larval stages of *C. haydeni* (Edwards).

C. haydeni inhabits open valley meadows in the central Rocky Mountains, principally in Wyoming and Montana (Ferris and Brown, 1981, *Butterflies of the Rocky Mountain States*). The larvae described here were reared from eggs laid by females caught at Granite Creek, Gros Vente Range, Wyoming on 7 July 1982 by P. F. Brussard and P. R. Ehrlich. The larvae were raised on various species of grasses in the tribe Hordeae. Descriptions of the first instar are based on 12 larvae, and the older larval description is based on one surviving third instar specimen.

First Instar

Head length 1.2 mm, width 0.7 mm; Lime green (8/6 on Munsell's (1929, *Munsell Book of Color*) color scale); hypognathous; six ocelli, third ocellus much larger than others; white tubercles distributed over most of the head. **Body** length 1.1 mm, width 0.5 mm; green-yellow green (7/6 on Munsell's color scale); five brown dorsal stripes from segments 4 to 11 with white bands (0.2 mm wide) bordering each stripe; all prolegs present; anal prolegs 0.55 mm long; anal plate bifurcate and reddish brown; crochets form a uniserial mesoseries; five white tubercles per abdominal segment.

### Mature larva (third instar)

Head length 1.4 mm, width 0.9 mm; green yellow (5/8 on Munsell's color scale); see Figure 1. **Body** length 7.2 mm, width 1.2 mm, green yellow (6/4 on Munsell's color scale), a lighter shade of green than head; anal plate with superanal spines reddish purple; three dorsal white stripes; two lateral white stripes, each bordered by a narrow band of purple-pink color (Fig. 2); crochets a uniordinal, uniserial mesoseries.

As with most butterfly larvae in later instars, primary setae are not distinguishable from the numerous secondary setae (see Figures 3a-c and 4a-b for distribution of setae). Note that setae are less dense on segment five than on segment 6 (Figs. 3b-c).

The larval stages of *C. haydeni* resemble those of other *Coenonympha* previously reported (loc. cit). They are typical of satyrids, having longitudinal stripes, bifid caudal appendages, and body and head covered with setae. Considering that they are abundant and easily reared, it is surprising that so few data exist on the early
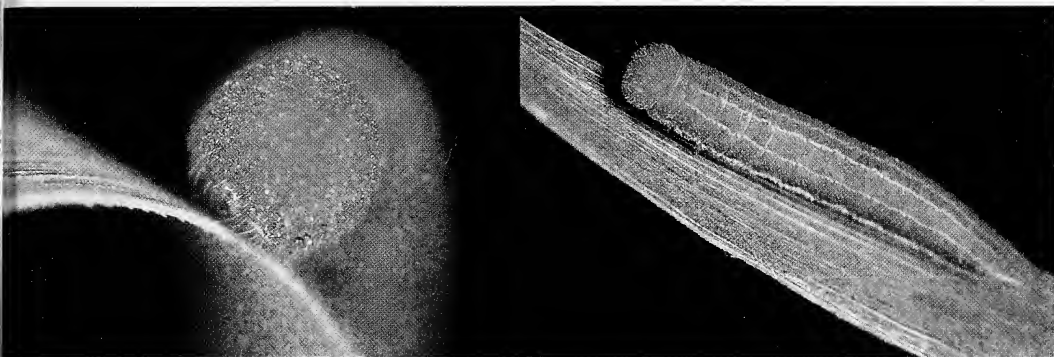
Figs. 1-2. Larva of *C. haydeni*. **1,** frontal view of head of third instar; **2,** lateral view of third instar.

5 mm
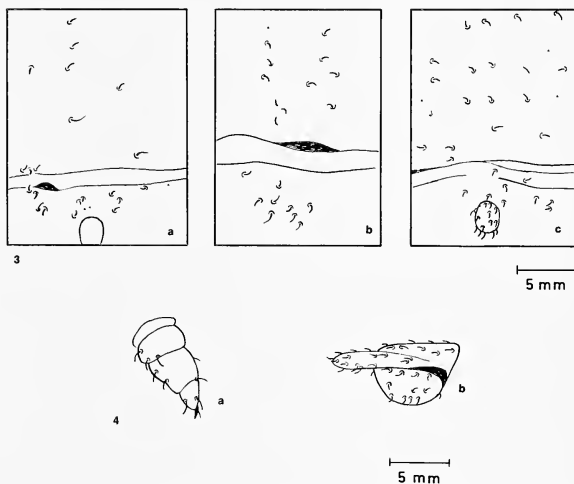
Figs. 3a-c, 4a-b. Distribution of setae of third instar larva of *C. haydeni*. **3a,** ventral view of segment 1; **3b,** ventral view of segment 5; **3c,** ventral view of segment 6; **4a,** lateral view of proleg 1; **4b,** lateral view of segment 11.

stages of these insects. Much more work needs to be done on all *Coenonympha* life histories.

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Obituary

Imagining Miguel Bustillo not alive is very difficult as he was one of those people who epitomized living, always animated and always on the go with endless projects underway. He was so active I never understood when he did the prodigious writing on Lepidoptera which he accomplished. I came to understand this was largely done in the early morning hours since most days were taken up with a vigorous law practice.

Although Miguel both was born (December 31, 1920) and died (December 17, 1985) in Madrid, a good part of his life was spent in Cuba. His family moved there in the mid-1950's to escape the civil war, and Miguel returned after the Cuban revolution in 1959. He had built a large international law practice in Havana, and, even knowing Castro and Guevara saw no alternative to leaving.

His early years with Lepidoptera were largely collecting. He left a large collection behind in Havana. His serious work and writing didn't start until 1969, but since then he generated over 180 papers. He also founded the Spanish Lepidoptera Society—SHILAP, and edited its *Revista*, which appears quarterly. He was principal author of "Mariposas de la Península Ibérica" of which five volumes have been published with nine more in various states of preparation. He also wrote "The Redbook of the Iberian Lepidoptera" (with Manuel Viedma), and "Las Mariposas de España". By any measure he was the leading figure of Spanish lepidopterology. In the recent past he was very active in conservation and served a key role in having the famous "El Regejal" site at Aranjuez declared a reserve.

Miguel's greatest strengths were his openness and generosity in bringing people together and encouraging work on Lepidoptera. He was very sensitive to propriety and in fact was troubled by some of the controversies the JRL generates. Given the famous feud between Miguel and Ramon Agenjo, this may seen strange, but then Agenjo and Miguel were reciprocal godfathers from an earlier deep friendship. When I last saw Miguel (we shared a room at the SEL Wageningen meetings in April 1984) he was very deeply troubled by Agenjo's death, which had been announced a few days before.

He leaves a charming, supportive wife, Sarita, and two lovely daughters. He also leaves a legion of co-workers who will never forget him.

INSTRUCTIONS TO AUTHORS

Manuscript Format: Two copies *must* be submitted (xeroxed or carbon papered), double-spaced, typed, on 8½ x 11 inch paper with wide margins. Number all pages consecutively and put author's name at top right corner of each page. If your typewriter does not have italic type, underline all words where italics are intended. Footnotes, although discouraged, must be typed on a separate sheet. Do not hyphenate words at the right margin. All **measurements** must be metric, with the exception of altitudes and distances which should include metric equivalents in parenthesis. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as example: 4. IV. 1979 (day-arabic numberal; month-Roman numeral; year-arabic numeral). Numerals must be used before measurements (5mm) or otherwise up to number ten e.g. (nine butterflies, 12 moths).

Title Page: All papers must have the title , author's name, author's address, and any titular reference and institutional approval reference, all on a separate title page. A **family citation must** be given in parenthesis (Lepidoptera: Hesperiidae) for referencing.

Abstracts and Short Papers: All papers exceeding two typed pages must be accompanied by an abstract of no more than 300 words. An additional summary is not required.

Name Citations and Systematic Works: The first mention of any organism should include the full scientific name with author (not abbreviated) and year of description. New descriptions should conform to the format: male: female, type data, diagnosis, distribution, discussion. There **must** be conformity to the current International Code of Zoological Nomenclature. We strongly urge deposition of types in major museums, all type depositions must be cited.

References: All citations in the text must be alphabetically listed under Literature Cited in the format given in recent issues. Abbreviations must conform to the *World List of Scientific Periodicals.* Do not underline periodicals. If four or less references are cited, please cite in body of text not in Literature Cited.

Tables: Tables should be minimized. Where used, they should be formulated to a size which will reduce to 4 x 6½ inches. Each table should be prepared as a line drawing or typed with heading and explanation on top and footnotes below. Number with Arabic numerals. Both horizontal and vertical rules may be indicated. Complex tables may be reproduced from typescript.

Illustrations: Color must be submitted as a transparency (i.e., slide) ONLY, the quality of which is critical. On request, the editor will supply separate detailed instructions for making the most suitable photographic ilustrations. Black and white photographs should be submitted on glossy paper, and, as with line drawings, must be mounted on stiff white cardboard. Authors **must** plan on illustrations for reduction to the 4 x 6½" page. Allowance should be made for legends beneath, unless many consecutive pages are used. Drawings should be in India ink at least twice the final size. Include a metric scale or calculate and state the actual magnification of each illustration as printed. Each figure should be cited and explained as such. The term "plate" should not be used. Each illustration should be identified as to author and title on the back, and should indicate whether the illustration be returned.

Legends should be separately typed on pages entitled "Explanation of Figures". Number legends consecutively with separate paragraph for each page of illustrations. Do not attach to illustrations. Retain original illustrations until paper finally accepted.

Review: All papers will be read by the editor(s) & submitted for formal review to two referees. Authors are welcome to suggest reviewers, and if received, submit name & comments of reviewers.
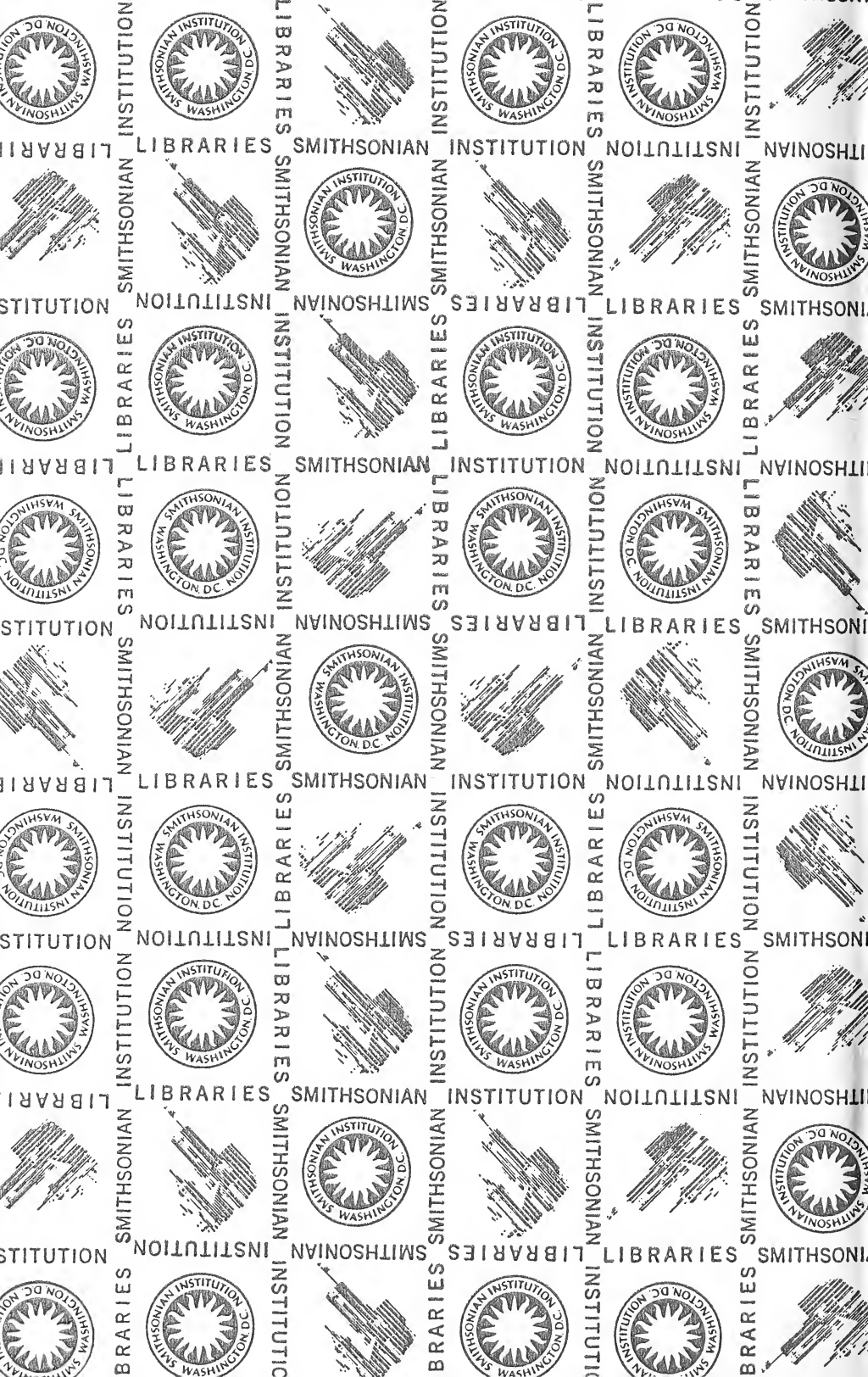
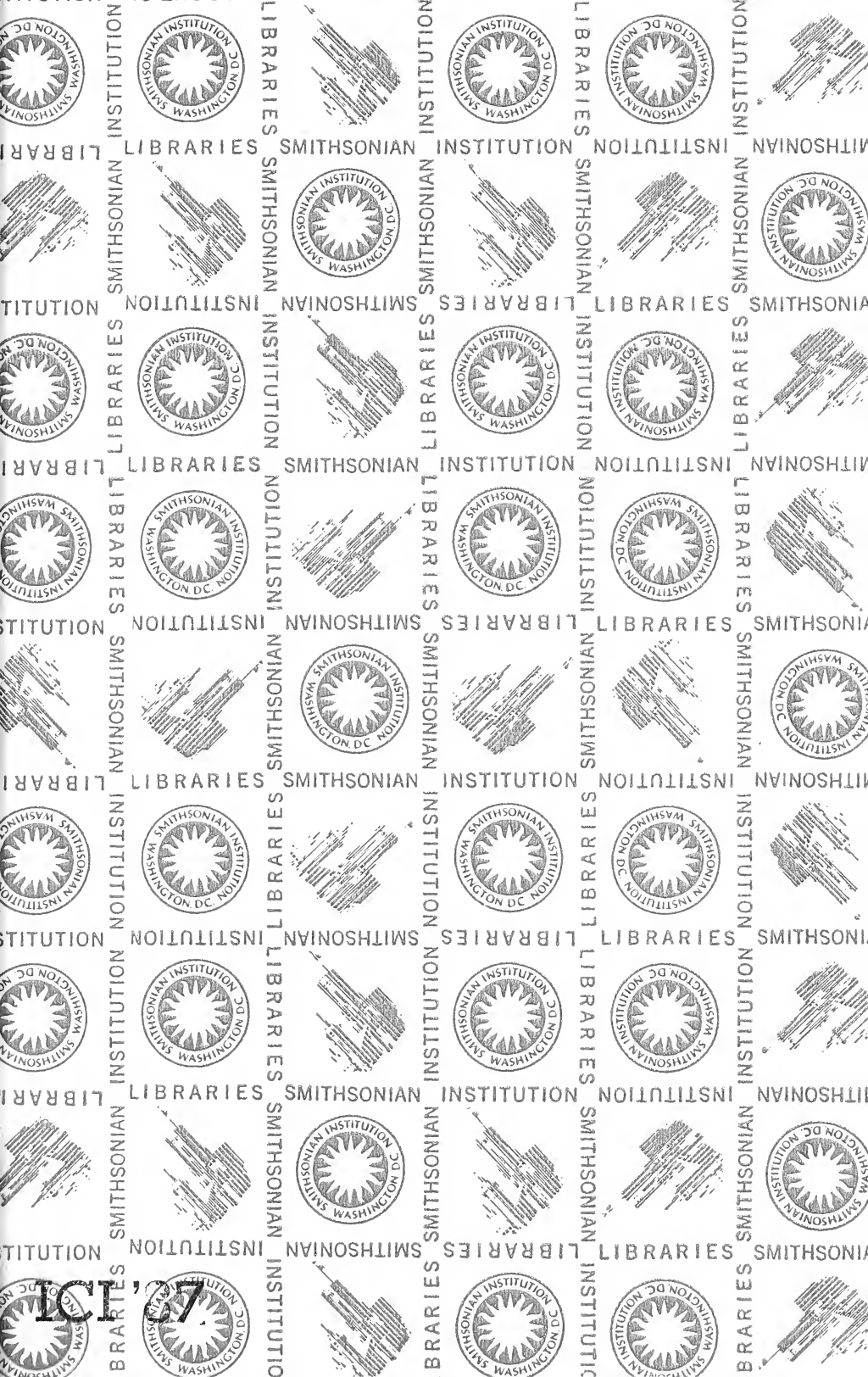# THE JOURNAL OF RESEARCH

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IN THIS ISSUE

COVER ILLUSTRATION: Photograph of Professor Zdravko Lorković with figures from two of his important works, see page 334.